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LIFE PROCESSES AND SIZE OF THE BODY AND ORGANS OF THE GRAY NORWAY RAT DURING TEN GENERATIONS IN CAPTIVITY

HELEN DEAN KING AND HENRY H. DONALDSON
THE WISTAR INSTITUTE OF ANATOMY AND BIOLOGY

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PART I. LIFE PROCESSES

HELEN DEAN KING

PART II. SIZE OF THE BODY AND ORGANS

HENRY H. DONALDSON

THE WISTAR INSTITUTE OF ANATOMY AND BIOLOGY

1929

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PART I. LIFE PROCESSES

HELEN DEAN KING

PART II. SIZE OF THE BODY AND ORGANS

HENRY H. DONALDSON

The Wistar Institute of Anatomy and Biology

TWENTY-TWO CHARTS

PREFACE

When it was recognized that the mutant albino rat differed from the ancestral gray Norway not only by the absence of pigmentation, but also in the proportional development of its organs, an attempt was made to feralize the Albino. This was done by planting Albinos where they might lead a wild life, in order to see how far, under these conditions, they would return toward the ancestral type. Five such colonies were planted in localities ranging from the Ipswich sands in Massachusetts to the dry Tortugas in the Gulf of Mexico, but for various reasons all of them failed. This first effort to determine whether the albino rat would revert, under wild conditions, to the gray Norway type, having thus met difficulties that halted it, the problem was revised, and it was next considered whether captivity and the accompanying treatment applied to the wild gray Norway might reduce it to the organ constitution of the Albino. Observations along this line seemed worth making, as we have no scientific record for any of our domesticated animals which show how domestication has changed them from the wild types from which they came.

Further, speaking broadly, no such tests are now possible, except perhaps in one or two instances, since the wild types are either unknown or for some reason not available, and consequently the data for comparison can hardly be had. In the case of the Norway rat, the gray form is definitely wild, depending on its own wits and exertions for its existence, while the albino mutant of the laboratory has now lived for many generations as a captive animal and may be fairly grouped with the other domesticated animals associated with man.

Consideration at once shows that continued captivity might be expected to alter the organ composition of the gray Norway. Such being the case, the alterations which prove to be similar to those now found in the Albino could be credited to captivity and treatment, while other modifications in the Albino not represented in the captive Norway could be referred to albinism.

It was on the basis of the foregoing considerations that the breeding of the Norway rat in captivity was undertaken by Doctor King in 1919. Naturally, this is a very long-time study which will require years for its completion. For this reason, occasional reports of progress seem to be permissible, and the following pages constitute an initial report of the observations on the first ten generations of the Norway rat in captivity.

INTRODUCTION

The purpose of this study is to determine such changes as may occur in the life processes and in the body and organs of the gray Norway rat when bred for a number of generations in captivity. In the case of the Norway rat, both the wild gray race and the captive albino race are readily available for study. When these are compared, marked differences in behavior and in the size of several organs are found. We wish ultimately to determine, in the case of the Albino, how far these differences may be due to prolonged captivity and how far to the condition of albinism—or possibly to other

causes, such as unconscious selection—applied to the albino strain. As contributory to this end, the effects of captivity on the wild gray Norway have been selected for study.

It may be remarked that the term 'captivity' is here used for the conditions under which the caged rats have been kept. The term 'domestication' has previously been employed to describe these same conditions, but as this latter term has wider connotations, such as a modification of the animal to meet human needs—which is absent in this instance—the term 'captivity' has been preferred, implying, as it does, merely a restricted range of activity and feeding, rather than foraging.

A general statement of the differences between the two races is given in "The Rat" (Donaldson, '24, p. 383). The wild Norways are more excitable and much more savage. They gnaw their cages. The body weight is less for a given body length, hence it is a slighter animal. The skeleton is relatively heavier, also the suprarenals (both sexes) and the testes and ovaries. The thyroid is of like weight, but the hypophysis distinctly lighter, in both sexes—this last difference being most marked in the female. On the other hand, the brain and the spinal cord are both heavier than in the Albino. The special relations will be noted as they come up for discussion.

It should be kept in mind that the present report applies only to the first ten generations of captive gray Norways, and is, therefore, a preliminary and tentative statement of results, since these data do not afford a basis for final conclusions. The observations are being continued and at present the nineteenth generation of these captive Grays has been obtained.

The selection of the first ten generations for treatment as a group depends on the fact that in the eleventh generation the strain 'broke' and several mutant varieties appeared, so that these ten generations are marked off by this event from those that follow.

In this paper the observations on the life processes are discussed in part I by King and those on the changes in the size and weight of organs and of the bones in part II by Donaldson.

Preceding these descriptions a statement is made concerning the conditions in the colony during the period under consideration. These conditions have an important bearing on the changes that have been observed.

The general care of the rats was not equally good during the period of seven years (1919-1926) which elapsed before the tenth generation was examined. In order to get at any effects of colony conditions on the captive Grays, the time relations of important events to the time relations of the several generations have been plotted in chart 1. In this chart each generation is represented by a vertical line running between the average date of birth, above, and the average date of killing, below. In individual cases, of course, birth preceded and killing followed the average date, but it was thought that this method of presentation would answer the present purpose of showing to what generations any particularly unfavorable conditions applied.

In the middle of 1922, the rats became infected with lice, and in September, 1922, were twice treated with larkspur solution for disinfection. This is a severe ordeal and, as the chart shows, affected younger animals in G_5 and G_6 and prospective mothers in G_7 .¹ In the summer of 1923, great heat prevailed for a time in the colony and could have affected most readily G_6 , G_7 , G_8 , as these individuals were at this time only half grown or younger.

From the middle of 1923 to the latter part of 1925, the care of the animals was not satisfactory, the caretaker being inefficient.

The observations to be reported show retardations in growth which apparently coincide with the unfavorable conditions represented by the louse infection, the larkspur treat-

¹ The successive generations are designated by G with a subscript giving the number of the generation in the series.

ment, and the excessive temperature of 1923. The effects of inadequate general care, as indicated on the chart, may also have been a factor contributing to the reduced body weights shown by the several generations from G_5 to G_8 .

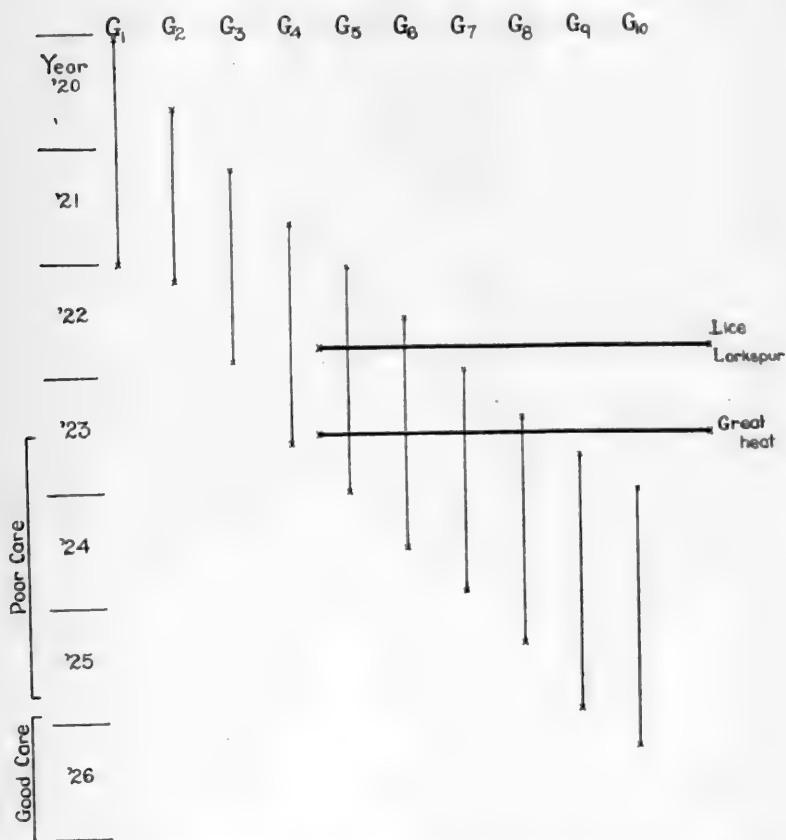
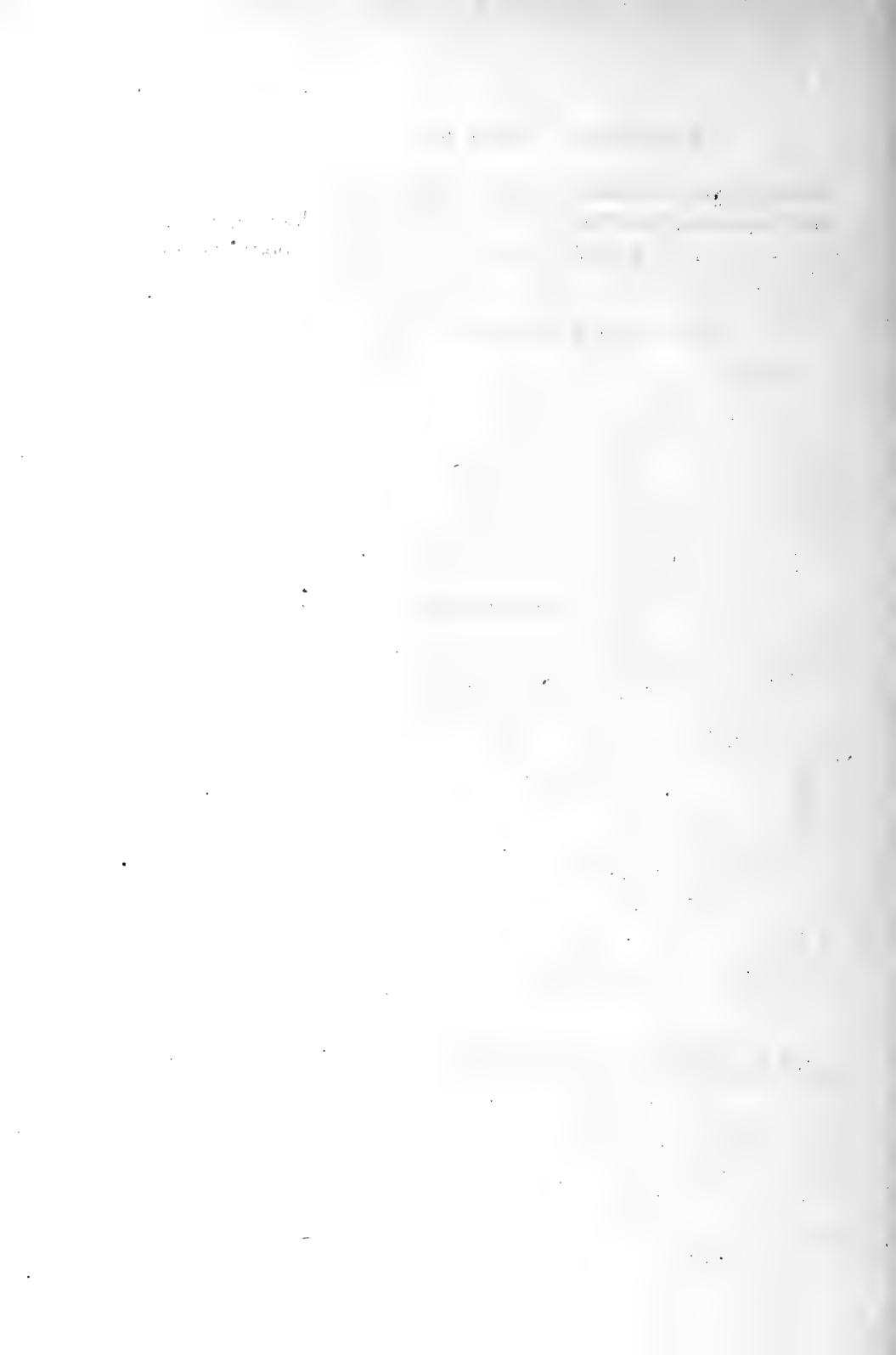


Chart 1 Showing birth date and killing date for each generation of captive Grays and indicating the incidence of unfavorable conditions.



PART I. LIFE PROCESSES

HELEN DEAN KING

MATERIAL AND METHOD

In the spring of 1919, thirty-six wild Norway rats were brought into The Wistar Institute Animal Colony to be used in starting a strain of captive Grays. These animals, comprising sixteen males and twenty females, had been trapped in various localities in the outskirts of Philadelphia, and all of them appeared to be vigorous and healthy. The smallest individuals were apparently about three months old at the time they were captured; the largest were adults at least a year old. In spite of the changed conditions of environment and of nutrition to which these rats were subjected, most of them lived for many months and some attained a body weight of over 400 grams.

Only six of the wild females cast young during the period of their captivity, as far as is known. From these females a total of twenty-one litters, containing 139 young (69 males and 70 females), was obtained. When breeding had ended, parents of litters were killed, measured, and carefully dissected; various organs were weighed, and certain bone measurements were taken. The findings were found to agree, in all essential respects, with those for a large series of wild Grays that Doctor Donaldson had examined previously. It is a fact of importance that this experiment was started with animals that were normal in every respect after months of caging, since it indicates that life in captivity for this period did not produce any marked changes in body structure. To what extent body functions were altered could not be determined, since practically nothing is known of life processes in wild Norways.

Wild gray females living in captivity show a pronounced tendency to destroy their young at birth, as Miller ('11) has noted. Casualties were so frequent with the litters cast by wild females in our colony that it was evident it would be impossible to obtain the animals needed to start a strain of captive Grays if the mothers were depended upon to rear their offspring. This difficulty was solved by removing the young rats from the nest as soon as they were discovered and giving them to a lactating albino female to rear. In a few cases albino females refused to suckle the substitutes for their own offspring, but in the majority of cases they accepted the young gray rats and reared them successfully. A total of 106 gray rats of the first generation, 51 males and 55 females, were brought to maturity and used for breeding stock.

That the early postnatal growth of gray rats that were suckled by albino foster mothers was not retarded is shown by a test made with a litter cast by a wild female that became relatively tame and did not greatly resent the temporary removal of her young from the nest. Four of the eight young in this litter were given to an albino female to rear; the other four young remained with the mother. At thirteen days of age the young suckled by the albino female weighed, on the average, 3 grams more than the other members of the litter. At thirty days of age, when all the rats were weaned, the average weight of those reared by the albino female was nearly 4 grams greater than that of the individuals their mother suckled. In later life, individuals of the same sex showed no pronounced differences in body weights.

Females of the first generation born in captivity did not show such a marked tendency to destroy their young as did their wild mothers. If the nest was disturbed very little when the young were removed for examination, they could be returned with a fair chance for life and future care. Individuals in the second and in all subsequent generations were reared by their own mothers.

In each generation about fifty individuals of each sex were reared for breeding and for a study of various life processes. The litters selected for this purpose contained an equal, or nearly equal, division of the sexes, and they were always of medium size (four to seven young) in order to avoid the possible effects of extreme litter size on body growth. Mortality among gray rats is often very heavy during the first few weeks of postnatal life, due to a variety of causes. In each generation, therefore, more litters were reared than the requirements of the experiment demanded, and those were discarded in which any individual died before reaching sixty days of age. Such a method of selecting breeding stock automatically eliminated weak individuals and assured strong, vigorous animals as parents of the following generation.

All of the captive Grays in the first ten generations lived under the same conditions of housing and of nutrition. Their food was a well-balanced, cooked ration composed of various cereals, meat, and vegetables; raw food, such as lettuce, carrots, cabbage, and fruit, was given two or three times a week. Variations in temperature to which these animals were subjected were not great. The colony room is adequately heated in winter and is relatively cool in summer. The cages that housed these rats were very large and therefore gave plenty of opportunity for exercise. The only unfavorable conditions affecting these rats were those referred to in the introduction.

All rats in the litters saved for breeding were weighed periodically. Birth weights were recorded if the young were obtained before they had suckled, otherwise the first weighing came at the age of thirteen days. The rats were weighed again when weaned, at thirty days of age, and thereafter at intervals of one month until they attained the age of twenty months. At this time a definite number of males was given to Doctor Donaldson for dissection, together with any females that had not cast a litter for at least two months. Females that were still breeding were kept for a longer time, in order that the litter records might cover the entire reproductive period.

BODY WEIGHT AT BIRTH

In the early generations of captive Grays parturition seemed to occur at night or in the early morning more often than during the working hours of the day; consequently, only a small number of litters were obtained before the individuals had suckled. Birth weights were taken for the twenty-six individuals in four litters cast by wild females. The twelve males in these litters had an average weight at birth of 5.34 grams; the average weight for the fourteen females was 5.09 grams.

In the first ten generations of these rats individual birth weights were recorded for a total of fifty-six litters, containing 177 males and 143 females. The average weights of the males varied from 5.07 to 5.82 grams in different generations; those of the females from 4.23 to 5.68 grams. There was no definite trend to the birth weights, either individual or average, as the generations advanced. In many cases individual females had a heavier weight at birth than one or more of the males in the same litter, but in each generation the average weight of the males exceeded that of the females. In fourteen litters of the tenth generation the forty-three males weighed, on the average, 5.29 grams at birth; the thirty-eight females had an average weight of 5.03 grams. These weights do not differ significantly from those of individuals in the first generation.

No other determination of the birth weights of gray Norway rats has been recorded, except that of Miller ('11), who states that the offspring of wild females in captivity weigh, on the average, 6.4 grams at birth, the males tending to be slightly heavier than the females. The number of individuals on which this determination is based is not given.

Apparently the weight of the gray rat at birth tends to be somewhat heavier than that of the albino rat. The findings of Jackson ('13) and of King ('15), for various series of Albinos, show that in this race the range of variation in the average birth weights of males is from 4.6 to 5.1 grams; that of females being from 4.5 to 4.9 grams. In both the

gray and the albino race of Norways, however, the average birth weight of the males, as a rule, exceeds that of the females.

Birth weight in the rat is influenced by a number of different factors, such as the age and physical condition of the mother, the size of the litter and its position in the litter series, and the length of the gestation period (King, '15). Environmental and physiological factors, therefore, may be largely responsible for the differences in the birth weights of gray and of albino young. To decide this point definitely will necessitate comparison between the birth weights of offspring from a large number of gray and albino females of various ages, and from litters of the same size. The collection of data for this purpose has been in progress for some years.

GROWTH IN BODY WEIGHT

There are two distinct phases of body growth in mammals, each of which consists of several growth cycles which merge into each other at transitional periods. The first of these phases comprises the period between conception and puberty, and in it the time rate of growth increases with the increase in body size. The second phase covers body growth during adult life, and here the time rate of growth decreases while the size of the organism increases (Brody, '26).

Our knowledge of the initial stage of the first growth phase in the rat, that occurring during fetal life, is based on the observations of Stotsenburg ('15), who studied the weight increase in albino fetuses from the thirteenth to the twenty-first day of gestation. During this period the percentage rate of growth per day was found to be approximately 53 per cent.

No study has been made, as yet, of embryonic growth in the gray rat. Data for the postnatal growth in individuals of the first generation of these captive Grays were published some years ago (King, '23), and they are here reproduced in tables 4 and 5. Points of interest in connection with these data will be discussed when comparison is made between them and the findings in later generations.

Although the males in the first generation of captive Grays were heavier than the females at birth, the latter grew more rapidly during early postnatal life. At thirteen days of age the average weight of the females exceeded that of the males by 0.9 gram, and was 3.6 grams greater at thirty days. The weight relation of the sexes was reversed, however, when the animals were sixty days old, and at all subsequent ages males were much heavier than females.

In his first study of body growth in the albino rat, Donaldson ('06) stated that males were heavier than females at birth and up to seven days of postnatal life, when a period of more active growth on the part of the females began. Growth graphs, constructed from data for the two sexes taken at intervals of one or two days, cross at the fourteen-day period, and that for the females runs above the one for the males until the sixty-day period. At this point the graphs recross, and that for the males runs at a higher level until its end. There is, therefore, a very striking similarity between the growth relations of the sexes in the strain of Albinos studied by Donaldson and those of individuals belonging in the first generation of captive Grays. Like relations were not found, however, in several subsequent studies on the growth of the albino rat (Jackson, '13; King, '15 a; Donaldson, '24), nor do they appear in the findings for the later generations of gray rats. In all of these cases the males have a heavier body weight than the females throughout the entire life span.

It seems probable that the differences in the weight relations of the sexes in these various series of Norway rats were due to environmental and nutritive conditions, not to factors inherent in the strains. At the time that Donaldson began his studies the rat was not as commonly found in biological laboratories as it is to-day, and little was known regarding the conditions necessary to maintain the animals in health and to enable them to grow and reproduce at a normal rate. Donaldson's rats were fed chiefly on milk-soaked bread and on corn, with the occasional addition of a little meat. Nutrition studies of later years (Osborne and Mendel, '16, '16 a,

'18, etc.; Slonaker and Card, '23; Evans and Bishop, '22, '22 a, '23; Kennedy, '26) have shown conclusively that rats require a well-balanced, highly nutritious diet for normal growth and for reproduction and that these animals respond very quickly to changes in nutritional regime. Males, seemingly, are more influenced by unfavorable conditions than are females, especially during fetal and early postnatal life, when the mortality among them is much greater (King, '21). It seems probable, therefore, that the slow growth of the males during early postnatal life in Donaldson's first series of Albinos was due to inadequate nutrition.

The growth relation of the sexes during early life in the first generation of captive Grays cannot be attributed to inadequate nourishment, since these animals received an abundance of highly nutritious food. Moreover, in the various strains of albino rats in the colony on the same nutritional regime, the growth of the males was more rapid than that of the females at all age periods. It must be assumed, therefore, either that the growth relations of the sexes during early postnatal life in the first generation of captive Grays was that normal for the race in its wild state or that lack of adjustment to conditions of life in captivity adversely affected the wild mothers of these rats and, through her, influenced the vigor of the young, particularly that of the males, so that they did not grow at a normal rate. Whichever of these alternatives one chooses to accept, it is certain that after one generation in captivity gray rats became so well adjusted to their new habitat that the course of body growth in their offspring showed the same sex relations at all age periods as those usually found in albino rats.

No marked changes occurred in the growth of the individuals in any of the first ten generations of captive Grays that made one generation stand out conspicuously from the rest. It seemed advisable, therefore, to combine the data for each three succeeding generations, beginning with the second, thus making three groups of data for nine generations. Data for the first generation stand alone, to be used

for comparison with the findings in later generations to indicate the changes in the rate and in the extent of body growth that resulted from life in captivity.

Weight changes in the body with age for individuals in the first group, comprising the second to the fourth generations, inclusive, are shown in table 1.

TABLE 1

Showing the increase in the weight of the body with age for individuals in the second to the fourth generations of captive gray rats

AGE IN DAYS	MALES				FEMALES			
	Number of individuals	Body weight in grams			Number of individuals	Body weight in grams		
		Average	Highest	Lowest		Average	Highest	Lowest
13	161	17	27	12	170	16	24	12
30	161	41	67	30	170	42	59	29
60	161	98	188	54	170	86	148	46
90	160	139	255	68	170	117	202	73
120	160	182	317	92	164	143	220	87
151	160	209	384	102	167	160	245	92
182	160	233	382	122	164	174	268	108
212	160	256	410	130	167	190	300	110
243	160	273	458	138	165	202	295	114
273	159	285	480	146	164	210	384	113
304	157	296	517	163	160	219	422	137
334	157	306	510	172	156	225	381	151
365	151	316	538	188	156	235	404	156
395	145	328	535	192	155	243	406	140
425	141	337	615	210	151	250	439	164
455	137	345	604	221	143	255	400	166
486	130	351	589	209	135	259	412	157
516	117	357	577	216	130	263	433	163
547	111	362	572	223	124	268	428	176
578	98	375	566	237	103	271	410	180
608	89	374	592	225	90	283	430	171

In the first group, as indicated by corresponding entries for the two sexes in table 1, the average weight of the males at thirteen days of age was only slightly greater than that of the females. At later age periods the excess in favor of the males increased greatly.

Although the average age at which the females of this group began breeding was 252 days (table 6), it is probable that the great majority of them had become sexually mature by the time they were six months old. At this age, which marks approximately the merging of the first growth phase into the second, the average body weight of the males was 59 grams greater than that of the females. This difference is 25.3 per cent, if the body weight of the males is taken as the standard in computation. In adult life both males and females became increasingly heavier, but the percentage differences in their weights changed but little. The maximum difference, 27.7 per cent, was reached when the rats were 578 days old.

As shown in table 1, no female in the first group attained a maximum weight exceeding that of a male of the same age, nor was the lowest weight recorded for any male below that for a female of like age.

Growth data are given in table 2 for the second group of captive Grays, comprising individuals in the fifth to the seventh generations, inclusive.

Differences between the average body weights of males and females during early postnatal life were about the same in the second group as in the first one (compare table 1 and table 2). At 182 days, however, males in the second group exceeded the females in body weight by only 47 grams, or 19.6 per cent. The maximum male excess in weight, 21.6 per cent, came at the age period of 578 days.

Maximum body weights for both sexes were higher in the second group than were those in the first group, and the average weights were greater at all age periods.

Data for the third group, including individuals in the eighth to the tenth generations, inclusive, are shown in table 3.

In the third group, as in the two preceding ones, sex differences in the average body weights were small during the early growth period, and increased as the animals grew older. The male excess in weight at 182 days was 42 grams (17.4 per cent), and its maximum (21.3 per cent) came at 578 days, as shown in table 3.

In each of the generation groups the percentage differences in the average body weights of males and females remained fairly constant throughout adult life, the variation being but 2 per cent in the first two groups and 4 per cent in the third group. These differences tended to decrease, however, as the

TABLE 2

Showing the increase in the weight of the body with age for individuals in the fifth to the seventh generations of captive gray rats

AGE IN DAYS	MALES				FEMALES			
	Number of individuals	Body weight in grams			Number of individuals	Body weight in grams		
		Average	Highest	Lowest		Average	Highest	Lowest
13	157	19	27	12	159	18	26	14
30	157	45	74	27	159	44	74	28
60	157	102	195	63	159	87	140	48
90	157	148	273	67	158	120	188	60
120	157	187	310	95	148	149	248	95
151	157	217	375	104	152	176	281	114
182	157	240	433	126	151	193	319	123
212	157	262	428	157	153	213	337	128
243	156	282	434	166	152	227	334	137
273	155	298	466	180	146	240	359	143
304	155	311	474	188	149	249	392	153
334	154	320	496	211	147	252	382	158
365	153	332	544	224	150	263	402	156
395	152	341	568	236	147	269	425	162
425	148	350	575	243	142	275	431	165
455	145	358	608	246	142	283	437	168
486	141	359	647	256	136	285	455	174
516	134	366	636	264	129	289	415	188
547	128	373	639	270	127	293	445	185
578	120	381	637	260	117	299	474	185
608	113	379	620	221	109	300	459	168

generations advanced. The male excess in weight in the third group was 7.9 per cent lower than that in the first group when the animals were 182 days of age, and 6.4 per cent less when the maximum was reached at 578 days. This progressive lessening in the percentage differences between the body weights of males and females was due, as a comparison of the

data in tables 1 to 3 shows, to the fact that body-weight increase during adult life tended to be greater in females than in males as the generations advanced. The increased weight of the females is to be attributed chiefly to the accumulation of fat in the body tissues, not to growth of the body as a

TABLE 3

Showing the increase in the weight of the body with age for individuals in the eighth to the tenth generations of captive gray rats

AGE IN DAYS	MALES				FEMALES			
	Number of individuals	Body weight in grams			Number of individuals	Body weight in grams		
		Average	Highest	Lowest		Average	Highest	Lowest
13	156	19	32	14	162	18	32	15
30	156	48	72	32	162	46	72	30
60	156	99	190	59	162	88	143	52
90	156	145	243	79	162	122	183	73
120	156	193	297	117	160	154	255	103
151	156	219	332	135	159	181	286	110
182	156	241	364	156	156	199	294	124
212	156	259	395	183	153	208	305	137
243	156	274	406	196	150	223	322	142
273	155	286	428	212	158	231	350	146
304	153	296	430	224	157	237	338	149
334	153	304	464	233	155	246	384	154
365	150	315	480	244	152	254	391	163
395	148	320	490	244	153	261	404	174
425	145	332	508	257	147	270	408	187
455	144	340	506	275	148	273	403	184
486	141	346	485	276	145	278	412	217
516	133	355	502	265	147	281	409	217
547	123	366	489	277	147	289	423	219
578	113	375	497	224	140	295	408	205
608	109	378	538	282	130	298	436	192

whole, since body length in females of the later generations was no greater than that in females of the earlier generations (table 12). Body growth of males during the second growth phase was apparently less influenced by the favorable environmental and nutritive conditions under which the animals lived than was that of females.

Since a graphic representation of the data will bring out more clearly the changes in body growth with age in successive generations of these rats, graphs for the growth of the males, constructed from data in tables 1 to 3, are shown in chart 2.

All three graphs in chart 2 run close together throughout their entire course, especially so at the beginning, where they have been separated somewhat more than the data warrant in order that individual graphs can be clearly followed.

The most important fact brought out in chart 2 is that body growth in captive gray males is accelerated during the period preceding puberty as the generations advance. The graph for the second group (fifth to seventh generations) runs slightly higher than that for the first group (second to fourth generations) from its beginning. The graph for the third group (eighth to tenth generations) crosses that for the second group at the 120-day period and then runs higher than either of the other graphs up to the 212-day period, subsequently falling to the level of that for the first group. The fact that males of the last group did not attain as heavy a weight in adult life as did those of the second group is not significant, since the growth of these rats during adult life was probably affected somewhat by unfavorable conditions in the colony (chart 1).

Growth graphs for the females in the three generation groups are shown in chart 3. These graphs were constructed from the data in tables 1 to 3.

Growth graphs for females (chart 3) differ from those males (chart 2) in two respects: 1) they are more widely separated throughout the greater part of their course; 2) all of them run at a lower level, since gray females are, on the average, much smaller than males at all age periods after weaning.

The graphs in chart 3 run very close together up to the 100-day period, when they begin to diverge. A progressive change in the form of the graphs as the generations advanced is not as clearly marked as in the case of the males. The

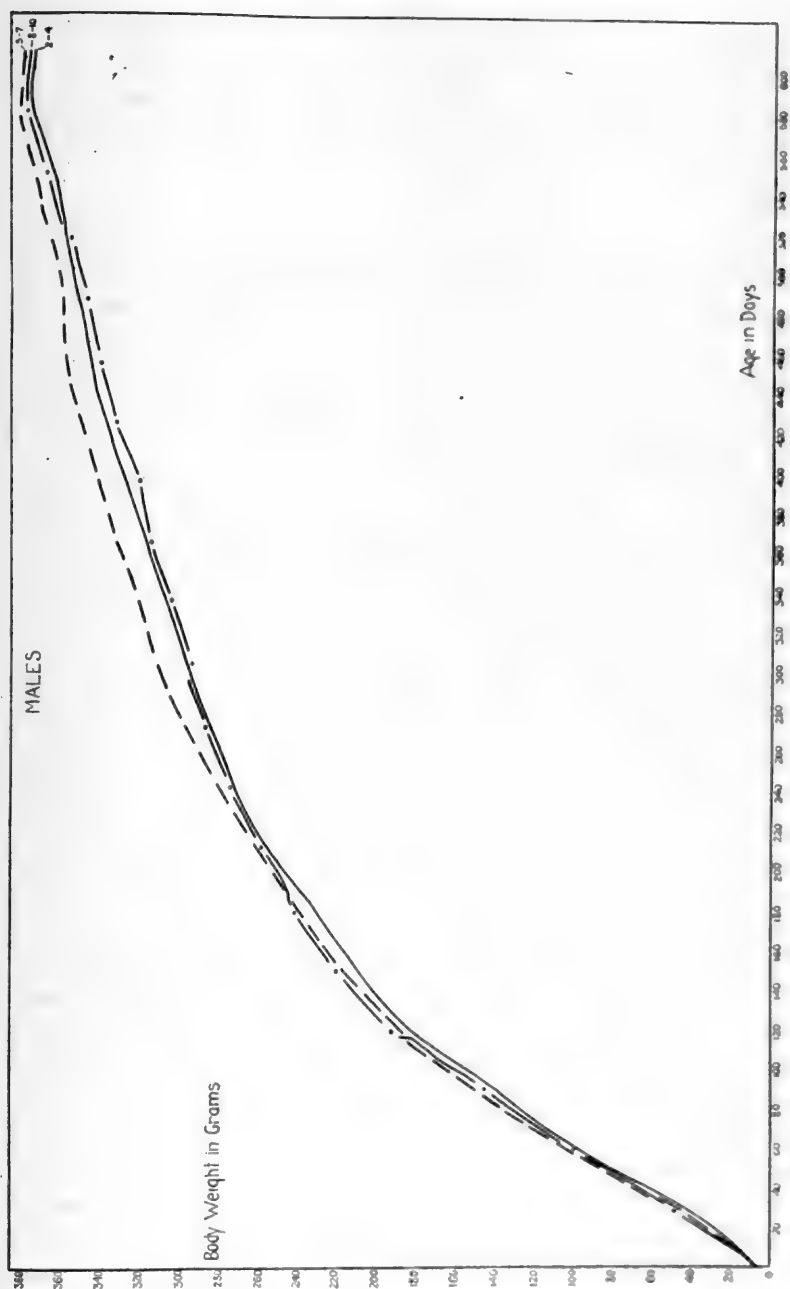


Chart 2 Graphs showing the increase in the weight of the body with age in successive generation groups of captive gray males.

graph for the third group of females, however, runs higher than either of the other graphs up to the 200-day period, thus indicating that females in the later generations had a relatively greater acceleration in body growth during the early portion of the life span than did females in the earlier generations.

Females in the later generations were heavier in adult life than were those in the earlier generations, as the position of the graphs in chart 3 shows. That the graph for the third group of females runs lower than that for the second group during the latter part of its course is due, doubtless, to the same cause as that advanced for a similar relation in corresponding graphs for males (chart 2).

In order to show the change in body growth of males that had occurred at the end of ten generations, data for body weights at different age periods for individuals in the first and for those in the tenth generation are given in table 4. The data for the first generation are reproduced from a previous publication (King, '23).

Data for average body weights, as given in table 4, are shown graphically in chart 4. This chart also contains a graph (3) for a series of stock albino males that were reared under similar conditions of housing as the gray rats, although they were fed on 'table scraps,' not on the ration that for some years has been given to all rats in the colony. Data from which graph 3 was constructed were given in a previous paper (King, '15 a, table 3).

In chart 4 the graph (2) for gray males of the first generation runs at a much lower level throughout its entire course than the graph (2) for males of the tenth generation. It shows no pronounced curve at its beginning, but mounts steadily upward and tends to be a straight line.

Graph 2, that for males of the tenth generation, is also a nearly straight line from its beginning up to about the 120-day period, when it curves upward. At the 240-day period the graph begins to flatten, and subsequently it runs fairly straight until its end. The space between graph 1 and graph

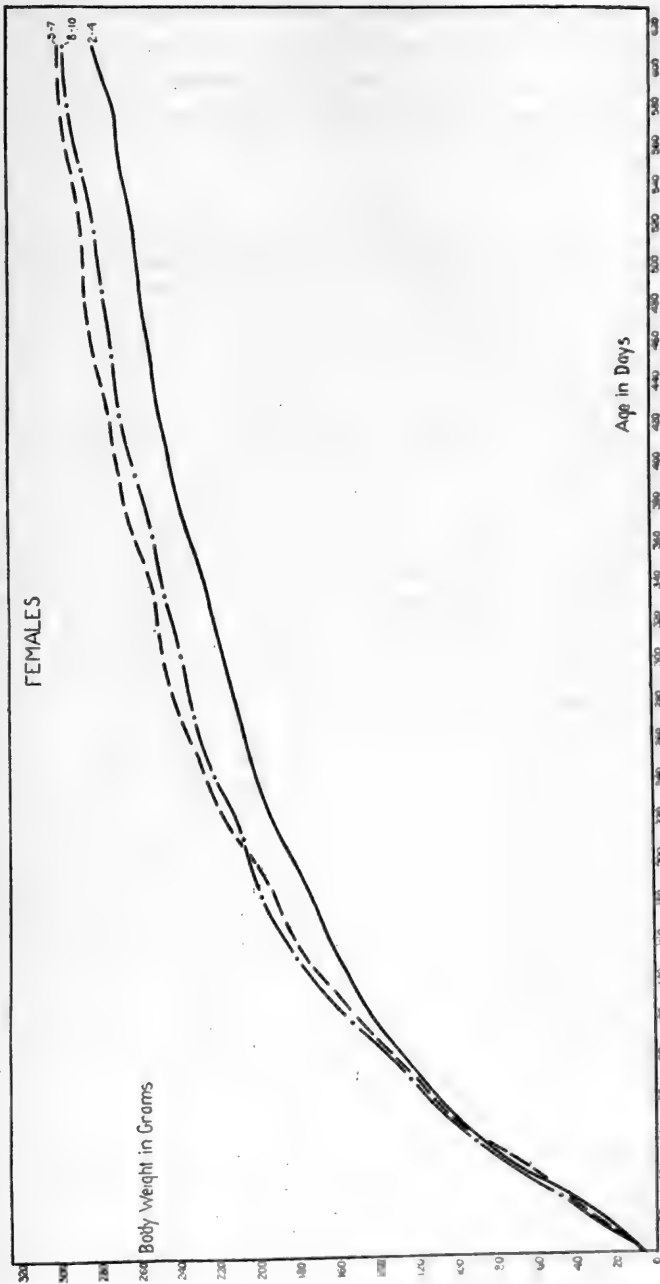


Chart 3 Graphs showing the increase in the weight of the body with age in successive generation groups of captive gray females.

2 at the 180-day period indicates a difference of 39 grams, or 19.9 per cent, in the body weights of these two series of males. At the end of the weighing period (608 days), the position of the graphs indicates a difference of 4.1 per cent in the body weights.

TABLE 4

Showing the increase in the weight of the body with age and the coefficients of variation for males in the first and in the tenth generation of captive gray rats, also coefficients for a series of stock albino males

AGE IN DAYS	FIRST GENERATION GRAY MALES					TENTH GENERATION GRAY MALES					STOCK ALBINO MALES
	Number of individuals	Body weight in grams			Coefficients of variation	Number of individuals	Body weight in grams			Coefficients of variation	Coefficients of variation
		Average	Highest	Lowest			Average	Highest	Lowest		
13	51	15.4	21	12	12.2 ± 0.82	50	20	32	16	15.3 ± 1.03	11.8 ± 0.79
30	51	33.4	41	26	13.0 ± 0.86	50	49	72	37	16.5 ± 1.11	10.2 ± 0.68
60	51	81.9	144	49	24.1 ± 1.60	50	92	161	59	24.3 ± 1.66	17.0 ± 1.14
90	51	115.9	201	68	26.2 ± 1.74	50	137	243	79	29.3 ± 1.98	14.8 ± 0.99
120	51	148.6	245	70	28.2 ± 1.88	50	180	277	126	22.6 ± 1.53	13.4 ± 0.90
151	51	176.1	284	87	24.2 ± 1.61	50	217	322	155	17.7 ± 1.19	13.3 ± 0.89
182	51	195.9	300	110	23.4 ± 1.55	50	235	364	177	16.5 ± 1.11	14.2 ± 1.22
212	51	218.4	330	128	21.8 ± 1.45	50	254	368	193	15.7 ± 1.06	14.0 ± 0.96
243	50	235.4	374	140	23.7 ± 1.60	50	268	398	209	14.2 ± 0.95	13.9 ± 0.99
273	50	253.5	379	154	22.4 ± 1.50	49	282	404	218	13.8 ± 0.94	13.4 ± 0.99
304	50	265.5	380	156	21.5 ± 1.45	49	290	410	230	12.1 ± 0.82	14.0 ± 1.11
334	50	276.7	395	170	19.8 ± 1.33	49	301	464	233	13.3 ± 0.91	13.7 ± 1.13
365	48	287.3	428	184	19.5 ± 1.33	48	312	480	246	13.2 ± 0.91	13.0 ± 1.16
395	48	297.4	442	185	19.5 ± 1.34	48	318	490	244	14.3 ± 0.98	12.6 ± 1.22
425	47	312.2	457	200	17.6 ± 1.22	48	327	508	263	14.0 ± 0.97	13.4 ± 1.32
455	47	322.3	471	188	19.2 ± 1.32	48	335	506	277	13.1 ± 0.89	13.6 ± 1.67
486	46	332.0	459	226	17.3 ± 1.21	47	346	485	279	12.1 ± 0.84	15.0 ± 2.06
516	43	335.0	476	226	17.4 ± 1.26	44	354	502	284	12.2 ± 0.87	
547	41	345.6	486	231	16.7 ± 1.24	41	368	478	284	12.1 ± 0.90	
578	39	358.0	516	233	18.3 ± 1.39	37	374	497	277	12.2 ± 0.95	
608	38	361.8	518	231	17.1 ± 1.32	34	377	538	303	14.5 ± 1.18	

The graph (3) for stock albino males has a distinctly different form from that of either of the graphs for gray males. At the age period from 40 to 150 days the graph has a very pronounced upward curve. Subsequently it flattens, and runs

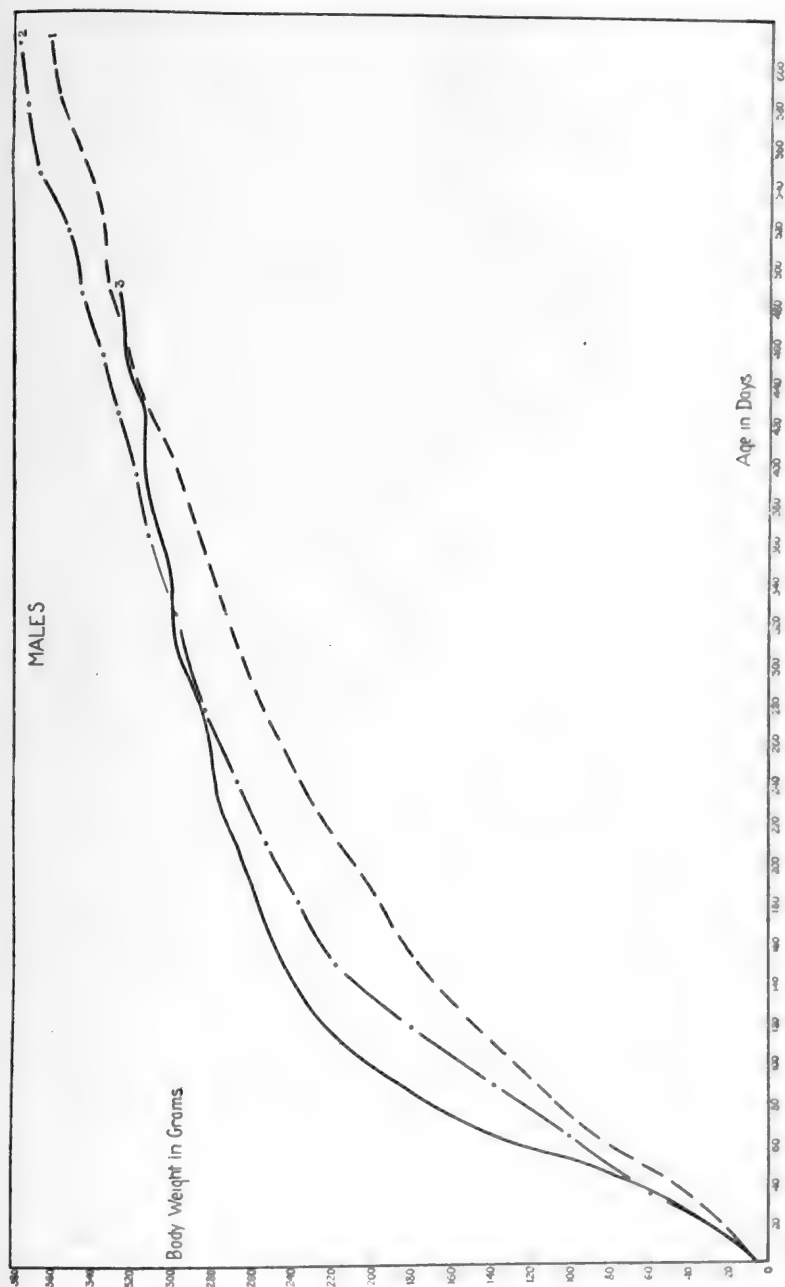


Chart 4 Graphs showing the increase in the weight of the body with age in series of male rats.

1. Graph for males in the first generation of captive Grays.

2. Graph for males in the tenth generation of captive Grays.

3. Graph for stock albino males.

nearly level until its termination at the 480-day period. Graphs might be constructed from available data for various other series of albino males that would, doubtless, have a slightly different course than that of the graph given in chart 4, but all such graphs would indicate very rapid growth during early postnatal life, which is, seemingly, characteristic for the albino race in general.

The relative positions of the graphs in chart 4 indicate that during the period of rapid growth, from 40 to 150 days, albino males were very much heavier than gray males of either series. At the 150-day period the space between the graph (3) for albino males and the graph (1) for gray males of the first generation represents a difference of 69 grams, or 28.2 per cent, if the body weight of the albino males is taken as the standard in computation. At this age period, however, albino males were only 28 grams, or 11.4 per cent, heavier than gray males of the tenth generation.

From the above analysis of data it is evident that the course of body growth in gray males had changed considerably at the end of ten generations of life in captivity. During the first growth phase the rate of growth was accelerated and was approaching the albino type. During the second growth phase the change was relatively slight, since the ultimate body weight attained by males of the tenth generation was only about 4 per cent greater than that of the males in the first generation.

Data for the increase in the weight of the body with age for females in the first and for those in the tenth generation of captive Grays are given in table 5.

In table 5 the findings for gray females parallel those for the corresponding series of gray males (table 4) in that they show that females of the tenth generation were heavier than females of the first generation at all age periods for which records were taken.

Chart 5 shows graphs constructed from the average body weights of gray females as given in table 5. In this chart, also, is a graph (3) for the body growth of albino females,

litter mates of the males whose body weights form the basis of graph 3 in chart 4.

The relative position and general trend of the graphs in chart 5 are much the same as those in chart 4, but all of them

TABLE 5

Showing the increase in the weight of the body with age and the coefficients of variation for females in the first and in the tenth generation of captive gray rats, also coefficients for a series of stock albino females

AGE IN DAYS	FIRST GENERATION GRAY FEMALES					TENTH GENERATION GRAY FEMALES					STOCK ALBINO FEMALES
	Number of individuals	Body weight in grams			Coefficients of variation	Number of individuals	Body weight in grams			Coefficients of variation	Coefficients of variation
		Average	Highest	Lowest			Average	Highest	Lowest		
13	59	16.3	21	12	14.6 ± 0.90	52	19	32	17	13.1 ± 0.90	11.4 ± 0.76
30	59	37.0	45	27	17.3 ± 1.07	52	47	70	35	14.1 ± 0.93	11.0 ± 0.74
60	59	75.2	110	47	19.8 ± 1.22	52	83	121	52	19.6 ± 1.09	15.7 ± 1.05
90	59	100.5	152	70	16.9 ± 1.04	52	117	183	73	23.8 ± 1.58	12.5 ± 0.95
120	59	122.6	184	77	16.0 ± 0.99	52	156	255	114	20.1 ± 1.33	10.3 ± 0.75
151	56	142.0	201	98	16.6 ± 1.03	49	186	276	128	16.5 ± 1.13	10.4 ± 0.73
182	54	153.5	256	111	17.8 ± 1.13	50	203	277	162	13.9 ± 0.94	12.3 ± 0.90
212	50	172.1	272	117	17.9 ± 1.20	50	212	298	164	14.1 ± 0.95	12.4 ± 0.91
243	52	189.3	278	133	18.2 ± 1.26	46	225	318	173	13.9 ± 0.98	12.6 ± 0.91
273	51	204.2	327	131	19.1 ± 1.27	50	234	363	186	17.0 ± 1.15	11.5 ± 0.89
304	47	209.8	301	123	19.9 ± 1.38	51	239	330	184	15.4 ± 1.03	10.3 ± 0.79
334	49	221.5	345	128	20.6 ± 1.40	50	247	360	181	16.4 ± 1.10	10.8 ± 0.87
365	47	232.8	344	152	20.4 ± 1.41	48	256	374	203	16.9 ± 1.16	10.7 ± 0.91
395	47	242.2	383	135	22.3 ± 1.54	49	258	388	188	17.3 ± 1.20	11.5 ± 0.98
425	43	247.5	380	156	21.1 ± 1.47	46	266	368	199	15.7 ± 1.10	10.9 ± 0.94
455	44	260.5	359	172	18.9 ± 1.35	48	268	385	209	15.2 ± 1.04	8.9 ± 0.99
486	43	257.9	382	182	19.5 ± 1.41	47	272	392	217	14.1 ± 0.98	13.4 ± 1.77
516	37	264.1	373	163	18.3 ± 1.43	48	275	400	219	14.8 ± 1.02	
547	36	261.5	375	173	19.4 ± 1.54	48	284	398	221	15.2 ± 1.04	
578	34	266.5	360	168	16.4 ± 1.34	46	291	403	224	16.0 ± 1.12	
608	31	271.9	339	184	15.3 ± 1.28	42	304	411	237	16.3 ± 1.20	

run at a lower level, since in both races of Norways the females, as a rule, are not as heavy as the males at any age period.

In chart 5 the graph (1) for gray females of the first generation runs below either of the other graphs and tends to be



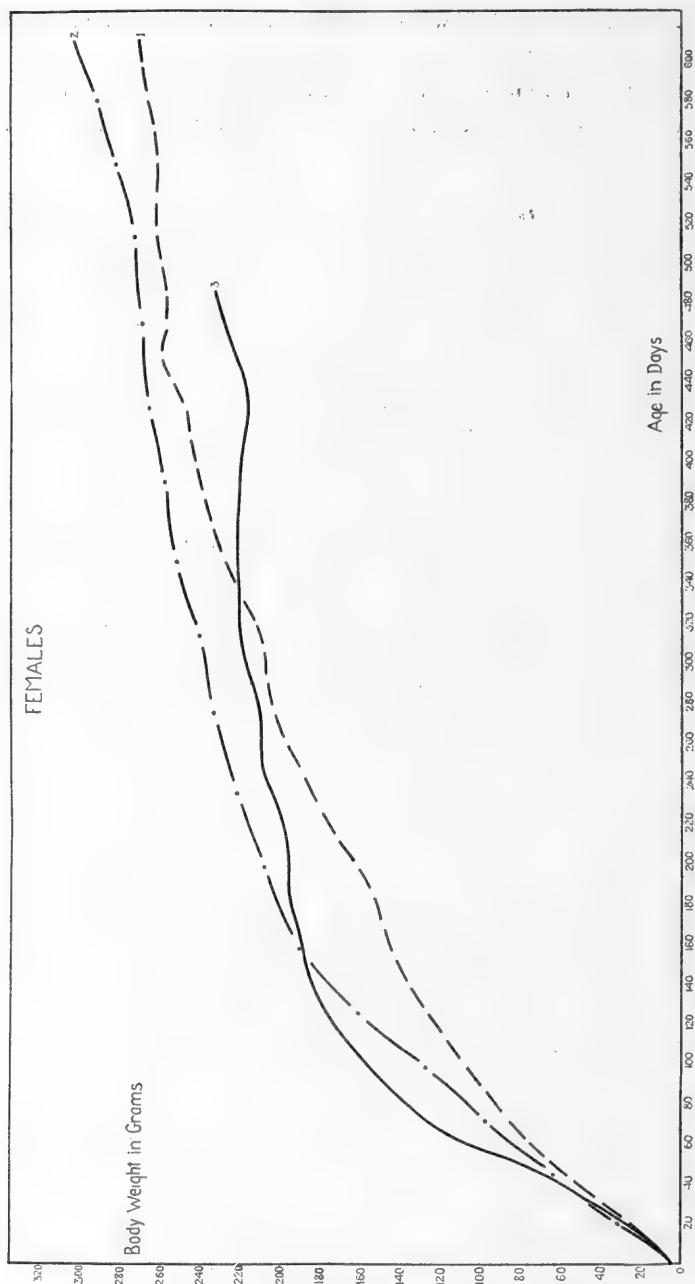


Chart 5 Graphs showing the increase in the weight of the body with age in series of female rats.

1. Graph for females in the first generation of captive Grays.

2. Graph for females in the tenth generation of captive Grays.

3. Graph for stock albino females.

a straight line, as these females showed no pronounced acceleration in body growth during early postnatal life. Graph 2, for gray females of the tenth generation, runs higher than graph 1 from its beginning until the end of its course. At the 150-day period the space between these graphs represents a difference of 44 grams, or 31 per cent, in average body weights. Subsequently these graphs run much closer, and their position at the end of the weighing period indicates a difference of but 8.1 per cent in the average body weights.

Albino females show the same marked acceleration in growth during the first growth phase as do albino males. In chart 5, as in chart 4, the graph (3) for Albinos runs much higher during the early part of its course than either of the graphs for Grays. At a later period, however, graph 3 flattens and falls below the level of the other graphs, since the albino females were not as heavy as gray females during adult life.

At 150 days of age albino females had an average body weight that was 44 grams, or 23.6 per cent, heavier than that of gray females of the first generation. At this age, however, gray females of the tenth generation had the same weight as that of the albino females, and they were much heavier in later life (chart 5).

The change in the rate and in the extent of body growth that had occurred in gray females at the end of ten generations of life in captivity was similar to that in the males. The trend was toward the type characteristic for albino rats in general. In only one series of Albinos for which data are available, that of Greenman and Duhring ('23), does the body weight of adult animals equal that of the tenth generation of captive Grays. These Albinos, however, were given exercise and were especially well cared for and fed.

The findings in these captive Grays are in accord with those for various domesticated animals, such as cattle, sheep, horses, etc., which are much larger at all age periods than their wild prototypes.

In the rat, as in the mouse and many other mammals, the period of most rapid growth ends at puberty, or very shortly afterward. The age at which sexual maturity was attained by gray females was not determined in any case by the exact method of Long and Evans ('22). The average age at which females of the first generation cast their first litters was 266 days; that of females of the ninth generation was but 200 days. In these rats, therefore, the beginning of reproductive life was advanced two months in the course of nine generations. Whether the more rapid growth of animals in the later generations induced earlier maturity or whether both the increase in the rate of growth and earlier maturity depended upon other factors is not known.

Robertson ('16) states:

The fact that the syntheses which constitute the growth of an organism are self-accelerated or autocatalyzed implies the existence of substances capable of acting as catalysers of growth. We know that many of the glands of internal secretion, anterior lobe of the pituitary, the thyroid, and thymus are capable of exerting important influences upon the processes of growth—influences the lack of which become apparent when one of the glands is removed.

It seems not improbable that the changes which life in captivity induced in the rate and in the extent of body growth in gray rats, and the effects of captivity upon breeding, were not related as cause and effect, but that both depended upon some alteration in the endocrine system which tended to speed up the growth processes and to induce earlier breeding as the generations advanced. It is interesting, in this connection, to note that the one endocrine gland in these rats most affected by life in captivity was the hypophysis which, as shown by Evans and Long ('22), is capable of influencing body growth in the rat. This gland is somewhat larger in both sexes of captive gray rats than it is in the wild form, and has tended to approach the albino type, as will be shown in a subsequent section (part II, p. 87).

It may be argued that the course of body growth in captive gray rats of the first generation is not representative

of the growth of wild rats in their natural habitat, and that conditions incident to captivity, the lack of exercise, changed nutrition, excessive fear, etc., greatly retarded early growth, which is probably very rapid in the wild form. On this assumption, the more rapid growth of individuals in the later generations would indicate merely that the animals had become somewhat adapted to their changed environment and were, therefore, resuming their normal rate of growth. Such an argument cannot be refuted at present, or probably at any time, since there seem to be insurmountable obstacles in the way of a scientific study of growth processes in wild Norway rats.

Aside from restricting activity somewhat, the conditions under which captive Grays lived would seem to be far more favorable to growth and to reproduction than are those to which wild rats are usually subjected. The element of fear could certainly not have influenced the growth of caged rats more than it must affect that of wild Norways which are constantly harassed by enemies of many kinds. The food given caged animals was more abundant and more nutritious than that wild rats obtain by foraging, and temperature conditions in the colony room were not as extreme as those in nature. Lack of exercise may possibly have influenced the later growth of caged Grays, but it could hardly have changed growth processes in young rats that spend the greater part of their time in the nest. Taking all of these various factors into consideration, it seems probable that the course of body growth in the first generation of captive Grays is fairly representative of that in the wild forms, and that it can be used legitimately to indicate the effect of captivity on the body growth of individuals in the later generations.

Since the albino rat is a mutant variety of the gray Norway, one may assume, perhaps, in light of the findings for captive Grays, that the rapid growth of Albinos during early life is a result of their long domestication. They have seemingly become completely adapted to life and conditions of captivity, and they have lost all fear of man, which is a dominant trait

in wild Norways. This lessening of nervous tension, and its far-reaching effects through the nervous system, may be a factor that influenced the course of body growth in gray rats of the later generations, since these animals were relatively very tame as compared with wild Norways.

VARIABILITY IN BODY WEIGHT

Since changes in the rate and in the extent of body growth in captive gray rats took place slowly, as shown in the previous section, it seemed probable that any change that occurred in body-weight variability was also a gradual one. Coefficients of variation for body weights at different age periods were computed, therefore, only for individuals in the first and for those in the tenth generations. A comparison of these two series of coefficients will indicate to what extent variability in body weight had changed at the end of ten generations.

Coefficients of variation, with their probable errors, for males in these two generations are given in table 4; those for females are shown in table 5. Each of these tables also contains a series of coefficients for body weights in the stock Albinos used for comparison with the Grays in the analysis of body growth. The coefficients for Grays of the first generation, as well as those for Albinos, are reproduced from previous publications (King, '15 a, '23). Grouped data had to be used in calculating the coefficients for the thirteen- and for the thirty-day periods, since only the average body weights for rats of each sex were recorded in the weighings of the litters at these ages. Coefficients for all other age periods are based on individual data.

Variability in body weight, as indicated by the size of the coefficients in table 4, had the same general trend in all three groups of males: it was relatively low in young animals, rose quickly to a maximum, and then fell gradually to a level that was maintained, with unimportant fluctuations, throughout adult life. At the various age periods, however, variability in body weight differed considerably in the three groups.

Gray males of the tenth generation tended to be somewhat more variable in body weight during early postnatal life than did males of the first generation, and maximum variability came at an earlier age (table 4). Since, however, differences between the maximum coefficients, and between corresponding coefficients for all age periods up to and including 120 days, are not statistically important, it appears that no significant change in body-weight variability had occurred during early life.

Variability in body weight during adult life had changed considerably at the end of ten generations. In males of the tenth generation variability decreased rapidly, after attaining its maximum at the ninety-day period, and subsequently was much less than that in males of the first generation. The size of the coefficient for the age period of 120 days indicates a drop of 6.7 ± 2.50 from the maximum; at age periods from 151 to 578 days differences between the corresponding coefficients for the two series are well over three times their probable errors. In a single instance such a difference would not be deemed of much statistical value, but the fact that this difference is found at fifteen consecutive age periods, covering about one-half of the life span of the individuals, adds considerably to its importance. The conclusion seems justified that gray males of the tenth generation were less variable in body weight during adult life than were males of the first generation.

A comparison of corresponding coefficients in table 4 indicates that gray males of the first generation were significantly more variable in body weight at all age periods from 60 to 395 days than were stock albino males. Gray males of the tenth generation showed a body-weight variability up to the age of 151 days that was greater than that in albino males of like ages, but variability in adult life was about the same in the two series. It is evident, therefore, that the trend of variability in captive gray males, as the generations advanced, was toward that found in stock albino males.

In gray females of the first generation variability in body weight did not reach its maximum at an early age, as in the other two series of females (table 5), but increased gradually until the 395-day period, after which it declined slightly. These females were more variable in body weight at all age periods, excepting at 90, 120, and 608 days, than females of the tenth generation, but differences between corresponding coefficients are small in most cases and therefore not significant. At the end of ten generations, variability in body weight had decreased but little in gray females. Comparison of corresponding coefficients for males and females in the tenth generation (tables 4 and 5) shows that variability in body weight was much the same in the two sexes, although the males tended to be slightly more variable in early life.

Although gray females in both the first and the tenth generations were more variable in body weight than albino females, the trend of variability with age in females of the later generation was more like that in albino females, since it reached its maximum at an early age and then declined (table 5).

There were two sources of error in the data for body weight in gray females that probably increased the size of the coefficients of variation for age periods during adult life. Data for a number of females carrying fetuses of sufficient size to add many grams to the mother's weight were doubtless included, since in gray rats pregnancy is well advanced before it is evident from casual observation: weights were never taken, however, if females were known to be carrying young. The data given include the body weights of females that were suckling litters. Lactation is a severe tax on the reserves of a female, especially if the litter is large, and the mother may lose considerable weight at this time. Such errors in the data cannot well be avoided if one is recording, at stated times, the body weights of breeding females; but, since they balance each other to some extent, they do not materially affect the average body weight at a given age for a large series of animals. They do, however, decidedly

influence the size of coefficients of variation for body weight that are calculated from individual, not from average, body weights.

It was not possible to determine the variability in body weight at birth in the gray rats used in this study. Coefficients of variation were calculated from the birth weights of 226 males and 212 females in seventy-one litters cast by gray females of the eighth to the tenth generation, inclusive, in order to obtain some idea of body-weight variability in newborn gray rats. The coefficient for the males was 12.83 ± 0.40 ; that for the females was 12.62 ± 0.42 . Variability in body weight at birth was, therefore, about the same in the two sexes. Birth weights in the males were slightly more variable than those in the females, ranging from 3.5 to 7.7 grams in the former and from 3.6 to 7.2 grams in the latter.

Data given above indicate that both in the gray and in the albino race of Norways males tend to be more variable in body weight than females during adolescence and early maturity. A slight, but constant, difference in body-weight variability of the sexes has been noted in other series of Albinos (Jackson, '13; King, '18, '19), and also in mice (Robertson, '16; Saller, '27). These observations are in accord with the theory, held by Darwin (1871) and by Brooks (1883), that throughout the organic world males, in general, are more variable than females.

In man, according to Boas (1897) and Porter ('05), variability in body weight is correlated with the growth rate. A like correlation was found in the stock Albinos used in this study, since variability was greatest at an age period at which growth was very rapid, and then gradually declined as the growth rate decreased during adult life. A rapid growth rate does not necessarily indicate a very high variability in body weight, however, as in both sexes of albino rats the body-weight variability was less than that in gray rats in which the growth rate was relatively slow during early life.

This same correlation is shown, also, by the data for the gray rats. In males of the first generation variability in body weight was highest at the time that the growth rate was most accelerated (60 to 151 days), and it showed no abrupt drop during early adult life when the rate of growth was decreasing but slowly. In these rats variability in body weight closely followed changes in the growth rate throughout life (table 4). In the females of this generation there was only a slight increase in body-weight variability at the sixty-day period when the rats were growing rapidly, and variability increased during adult life when the growth rate was decreasing. In both sexes of gray rats of the tenth generation the correlation between growth rate and body-weight variability was as marked as in the Albinos.

Darwin (1875) was of the opinion that all domesticated animals, with rare exceptions, vary far more than animals in a wild state. He states:

Variability of every kind is probably directly or indirectly caused by changed conditions of life, or put another way, if it were possible to expose all the individuals of a species during many generations to absolutely uniform conditions of life there would be no variability.

Had the science of genetics been developed during Darwin's time, he would doubtless have modified many of his views, including that of the cause of variability.

In gray rats that have lived for a number of generations in captivity under fairly uniform environmental conditions variability in body weight has tended to decrease. Such a result was to be expected if, as seems probable, some part of this variability was due to the action of factors inherent in the individuals themselves.

Our colony of gray rats is, in a sense, an inbred colony, since no new stock has ever been added and all of the rats have descended from six wild females. These rats have not been very closely inbred, however, since it has always been the rule to select litters for weighing and for breeding stock that were the offspring of parents not closely related. Such a system of breeding would, no doubt, gradually lessen the

variability in body weight due to the action of genetic factors, as the individuals would tend to become more homozygous as the generations advanced. Close inbreeding does not reduce variability in body weight very rapidly, as is shown by the fact that albino rats, inbred brother and sister from the same litter for twenty-five consecutive generations, showed at the end of this period a variability in body weight at different age periods that was but little less than that in outbred albino controls. In these inbred Albinos, however, changed conditions of nutrition undoubtedly acted to increase the variability in body weight in individuals of the later generations (King, '18, '19).

In a given litter of rats the birth weights of members of the same sex often show considerable diversity, and they may differ by more than 100 per cent. Individuals in the litter tend to maintain the order relation in their weights at birth throughout life, as Dunn ('08) determined for albino rats and as records for a large number of litters in different series of rats in our colony show. There are, of course, exceptions to this rule, but they seem to be due, in most cases, to a change in the physical condition of the individuals that is caused by disease or by an excessive accumulation of fat. When rats are very small at birth, their growth seems to be inhibited from the beginning of postnatal life by causes that are constitutional. This is shown in the case of the so-called 'runts' that are found frequently in litters of rats. In these individuals growth continues at a slow rate for some time, but no matter how much care is given, they never exhibit normal vigor, nor do they ever attain the body size normal for a given age (King, '16).

Female rats of the same age, living under similar conditions of environment and of nutrition and breeding at the same season of the year, may cast litters of like size in which the individuals of the same sex show marked differences in their birth weights. On comparing the later growth of such individuals, it has been found that the weight differences at birth are indicative of unlike growth capacities, and that the

rats with the heavier weights at birth tend to maintain their supremacy at all age periods. While variations in the length of the gestation period may account for the unlike birth weights of the members of these litters, they cannot explain the differences in the growth rate and in the ultimate body weights attained which must be due to constitutional causes.

There is, moreover, a constant, though small, sex difference in the birth weights of rats, males tending to be heavier and slightly more variable than females. This sex difference persists throughout life and becomes greater as the individuals grow older, even when environmental and nutritive conditions are the same for all animals. Seemingly, body-weight variability at birth and that found at all age periods during postnatal life in individuals of the same sex, as well as in those of different sex, are indicative of differences in growth capacity which depend, in large measure, upon constitutional causes. Saller's ('27) statement regarding the cause of variability in the body weights of the mouse is doubtless applicable to many, if not to all, animals:

In der Anlage der Tiere, also genotypisch begründete Unterschiede im Gewichtsverlauf und damit auch für die von ihr erreichte Endgrösse bestehen.

There are, however, many factors that are not genetic that unquestionably influence body weight in the rat and so tend to increase its variability. The age and physical condition of the mother, the size of the litter, and the length of the gestation period, all affect the fetal young and so contribute to the variability found in the birth weights of the newborn (King, '15). In some cases, also, all of the ova liberated at a given period of ovulation are not fertilized at the same time, as is shown most convincingly when superfecundation occurs (King, '13). The advantage thus given to some of the embryos likewise tends to cause variations in the weights at birth.

During postnatal life the growth rate and also the variability in body weight at different age periods are influenced considerably by temperature, nutrition, housing conditions,

amount of exercise, etc. Unfortunately, no way has been found, as yet, to determine how much of the variability shown is due to genetic factors and how much of it depends upon environmental, nutritive, and physiological causes.

With environmental and nutritive conditions as uniform and as favorable as it was possible to make them, with temperature changes in the colony relatively small, and the housing conditions such that the rats could obtain considerable exercise, it would seem that factors such as these could have had but little effect on the growth rate and on the variability in body weight of the captive gray rats. Physiological factors acting during prenatal life could not, of course, be controlled, and they undoubtedly were responsible for much of the variability found in the birth weights. The variability shown at all age periods during postnatal life, however, was probably due, in part at least, to differences in the genetic constitution of the individuals.

THE REPRODUCTIVE PERIOD

Little is known regarding the reproductive life of gray Norways living in their natural habitat. According to Miller ('11), offspring of wild parents, born and reared in captivity, attain sexual maturity at least by the end of the fourth month. Eaton and Stirrett ('23), in agreement with Lantz ('10), maintain that wild gray rats mature at about three months of age and that breeding continues until the animals are about twenty months old. These investigators, however, give no data in support of their assertions. The youngest of the wild rats used as foundation stock for the captive Grays in our colony must have been at least six months old before they began to breed. Possibly the changed conditions incident to captivity retarded the onset of puberty and so delayed reproduction.

In this study the reproductive life of any gray female is considered to have begun with the birth of the first litter for which a record was obtained. Since females of the earlier generations often destroyed their litters at or soon after

birth, there is the possibility that litters were cast which were not recorded. There is the same possible source of error in the data for the last litters cast, as offspring of old females are often born dead and are eaten or lost in the debris of the cage. It has always been part of the routine work in the colony to examine cages containing breeding animals at least once a day in order to make the litter records as complete as possible.

TABLE 6

Showing length of the reproductive period in days in different generations of captive gray rats

GENERATION OF BREEDING FEMALES	EARLIEST AGE AT WHICH A LITTER WAS CAST	LATEST AGE AT WHICH A LITTER WAS CAST	TOTAL LENGTH RE-PRODUCTIVE PERIOD	AVERAGE AGE WHEN FIRST LITTER WAS CAST	AVERAGE AGE WHEN LAST LITTER WAS CAST	AVERAGE LENGTH RE-PRODUCTIVE PERIOD
1	144	702	558	266	470	204
2	141	690	549	244	434	190
3	95	586	491	247	431	184
4	111	578	467	210	444	234
5	117	582	465	230	452	222
6	93	581	488	186	406	220
7	97	703	606	242	494	252
8	120	596	476	209	495	286
9	96	646	550	200	450	250
Average	112.6	629.3	516.6	226.0	452.9	226.9

A summary of the data for the reproductive period in females of the first nine generations of captive Grays is given in table 6. Reproduction in females of the tenth generation will be discussed in a future paper.

Only one of the thirty-seven fertile females in the first generation born in the colony cast a litter before she was five months of age; many of them did not bear young until they were over a year old. The average age at which these females began breeding was 266 days, or approximately nine months. As the generations advanced, breeding began at an earlier age, and in the later generations some of the females cast litters when they were less than four months old.

The average ages at which the first and the last litters were cast by females of the different generations are shown by graphs in chart 6. The graphs were constructed from data given in table 6.

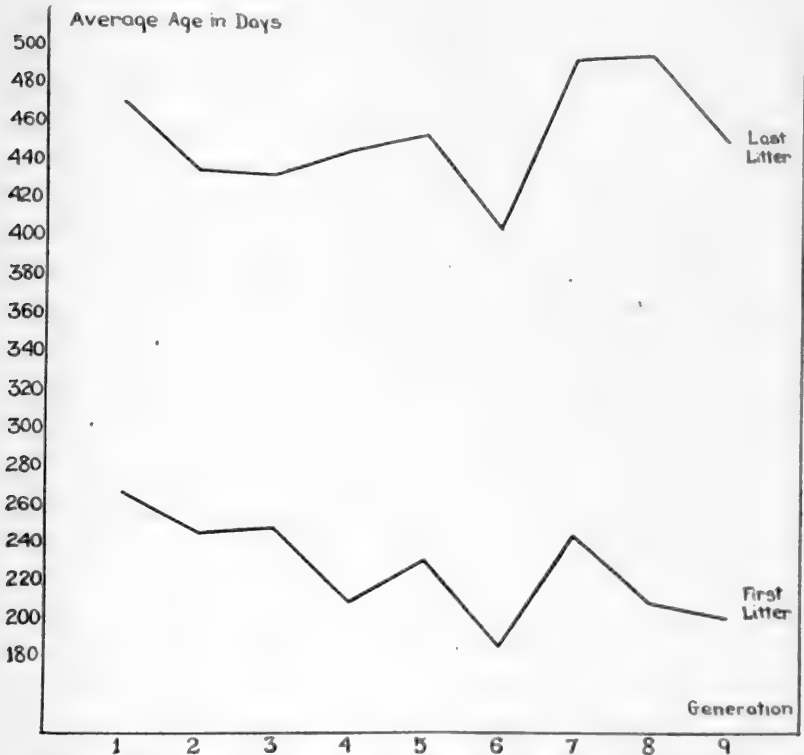


Chart 6 Graphs for captive gray females, showing the average age when the first and when the last litter was cast.

As indicated by the course of the lower graph in chart 6, the average age at which females cast their first litters tended to decrease from the first to the sixth generation. The late beginning of reproduction in females of the seventh generation was due, probably, to the fact that these females did not receive as adequate care as did those of the earlier and of the later generations. With the improvement in general conditions, the females again began breeding at a relatively early

age, as the downward trend of the graph indicates. In females of the ninth generation, reproduction began, on the average, two months earlier than in females of the first generation. The onset of reproductive life in females of the last generation, however, was still considerably later than that in albino females, which cast their first litters, as a rule, when they are about three months of age. It would appear, from the data obtained, either that gray females became more adapted to their changed environment as the generations advanced and so began breeding at or near the time normal for the beginning of reproduction in wild Norways, or, as seems more probable, that life in captivity hastened the beginning of reproductive life, as has been the case in many domesticated animals (Buffon, 1832; Darwin, 1875).

There were marked individual differences in the time at which the menopause appeared in these rats. Many females ceased to bear young after they had cast two or three litters, although they were seemingly in good physical condition; other females continued to breed until they were nearly two years old. While the total length of the reproductive period varied considerably in different generations, as shown in table 6, the variations showed no definite trend as the generations advanced. The average age of the females when the menopause appeared is shown by the upper graph in chart 6. The course of this graph, in general, is much like that of the lower graph on the same chart.

There are, apparently, no definite limits to the reproductive period in female rats. Its length depends, as do growth and many other life processes, on the interaction of a number of different factors. Not only environment, but also the physical condition of the animals, influences reproduction. One factor of paramount importance is the lung infection which frequently attacks rats of both sexes after they are a year old. This disease is not immediately fatal, but it soon puts an end to breeding and so materially shortens the reproductive life of its victims.

The changes in the average length of the reproductive period as the generations advanced are indicated by the graph in chart 7, constructed from data in table 6.

A change in the average length of the reproductive period at the end of three successive generations is indicated by the course of the graph in chart 7. The rise in the graph at the fourth generation denotes an increase of thirty days over the length of this period in females of the first generation.

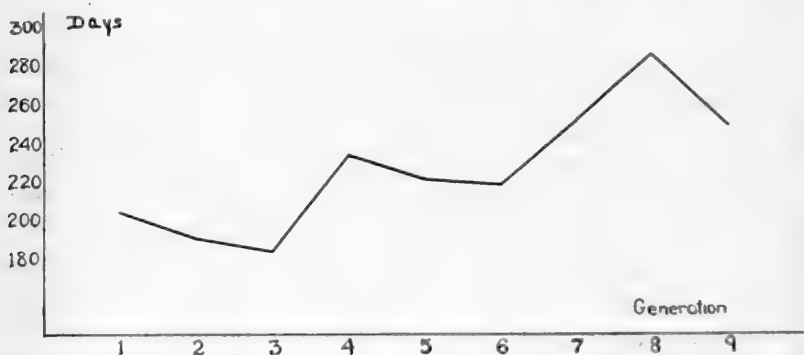


Chart 7 Showing the length of the reproductive period in different generations of captive gray females.

Another upward turn in the graph at the seventh generation is indicative of a further gain of thirty-two days. The highest point in the graph, at the eighth generation, marks a reproductive period extending over 286 days. The average reproductive life of females in the last three generations was seventy days longer than that in females of the first generation.

From the data presented in this section, it appears that the duration of reproductive life in gray females changed considerably in the course of nine generations. Breeding began at an earlier age as the generations advanced, therefore the average length of the reproductive period was increased in later generations by about two months.

FERTILITY

It has long been known from the writings of Buffon (1760), Geoffroy Saint-Hilaire (1862), and Darwin (1875) that domesticated animals, as a rule, are more prolific than their wild representatives. To what extent fertility has been increased has not, however, been determined with certainty for any species, since data for wild forms are meager and, from a statistical standpoint, cannot be considered as adequate for purposes of comparison.

In the rat fertility may be measured both by the number of litters cast and by the number of offspring produced by breeding females during their reproductive life. There are but few statements in literature regarding litter production in wild gray Norways. Zuschlag ('03) assumes eight litters a year to be the average produced by a single pair of rats. Lantz ('10) states that Norway rats probably breed from three to five times a year, while Miller ('11) estimates that five or six litters may be reared yearly. Eaton and Stirrett ('28), from an investigation of the rat population in New Bedford, Massachusetts, are of the opinion that females produce from three to four litters a year. The limitation of numbers in nature is accomplished by a restriction of the reproductive rate, probably through the influence of nutrition, as well as through the action of natural enemies. That inadequate nutrition has a marked effect on reproduction in the rat has been shown by the investigations of Osborne and Mendel ('17), Evans and Bishop ('22 a), and Slonaker and Card ('23). It is to the copious food supply, without the labor of seeking it, that Darwin (1875) attributes the greater fertility of animals under domestication.

The average size of the litters in wild rats has been variously estimated by different investigators. Zuschlag's theoretical table gives eight as the litter average. According to Crampe (1884), Lantz ('10), and Miller ('11), litters contain an average of ten young. Lloyd's ('09) observations on pregnant rats in India showed that litter size ranged from one to twelve, with the average about six. Instances of twenty-

two to twenty-four young in a single nest have been recorded, but there is no evidence that these young were the progeny of a single female. The average number of fetuses in a large number of gravid females captured in India was 8.1 (Lantz, '10). As many as sixteen fetuses were found in wild Norway females by Zuschlag, by Lantz, and by Donaldson ('24). Since many fetuses are absorbed in situ, as Huber ('15) and Long and Evans ('22) have shown, the number of fetuses found in gravid females is not indicative of the number of young that

TABLE 7

Showing litter production and average size of litters in different generations of captive gray rats

GENERATION OF BREEDING FEMALES	NUMBER OF BREEDING FEMALES	TOTAL NUMBER LITTERS	AVERAGE NUMBER LITTERS PER FEMALE	TOTAL NUMBER YOUNG	AVERAGE NUMBER YOUNG PER LITTER
Wild grays	6	21	3.50	139	6.62
1	37	143	3.86	857	5.99
2	42	114	2.71	691	6.06
3	44	142	3.23	849	5.98
4	50	191	3.82	1202	6.29
5	46	176	3.83	1084	6.16
6	48	192	4.00	1167	6.08
7	48	169	3.52	1063	6.27
8	48	210	4.37	1293	6.16
9	48	181	3.77	1160	6.40
	417	1539	3.69	9505	6.17

will be born. All of these observations were made on females of unknown ages, and they give, therefore, no evidence regarding litter production or the average litter size during the reproductive life of the females.

Data showing fertility of females in the different generations of captive Grays are given in table 7.

The breeding record for wild gray females, as given in table 7, may be very incomplete, since some of the females were obviously several months old when they were brought into the colony, and they may have cast young previously to this time. The data for these rats, however, are quite in ac-

cord with those for gray females of the later generations, and they doubtless cover the greater part, if not all, of the offspring produced.

For the entire series of 417 breeding females in the first nine generations of captive Grays, the average number of litters per female was 3.69, and the deviation from this mean in any generation was relatively slight. The largest number of litters cast by any of the females was ten; the smallest number was one. Conditions of captivity, although affording abundant food and protection from enemies, did not increase the average number of litters cast as the generations advanced.

It may be assumed, perhaps, that breeding was restricted in these gray females by the fact that the animals were not completely adapted to conditions of captivity, and therefore did not reproduce at the rate normal for the race in its natural habitat. Since no adequate data for wild Grays are available for comparison, definite conclusions regarding this point cannot be drawn. The average number of litters cast by captive gray females was considerably less than that in a large series of stock Albinos, reared under similar environmental conditions, where the females produced an average of 5.5 litters (King, '24).

The estimation of eight to ten young as the litter average in wild gray rats is undoubtedly much too high, if applied to the entire litter output of any single female or of any group of females. In both the gray and the albino race of Norway rats litter size changes with the age of the female, and litters cast at the beginning and at the end of the reproductive period are much smaller than those cast during the height of breeding activity.

For the entire series of 1539 litters in the first ten generations of captive Grays the average size of the litter was 6.17, and the deviation from this mean in any generation was not significant (table 7). This average accords with the finding of 6.3 young per litter in stock Albinos (King, '24). The range in litter size was from one to fourteen, the largest lit-

ters, as a rule, being cast by females that were from ten to twelve months old.

The trend in litter size as the generations of gray rats advanced is shown graphically in chart 8. The graph was constructed from the data for average litter size given in table 7.

The highest point of the graph in chart 8 is at its beginning, since the litters cast by wild females were, on the average, somewhat larger than those cast by females in the later generations, probably because wild females did not begin breeding until they were relatively old. At the second generation the

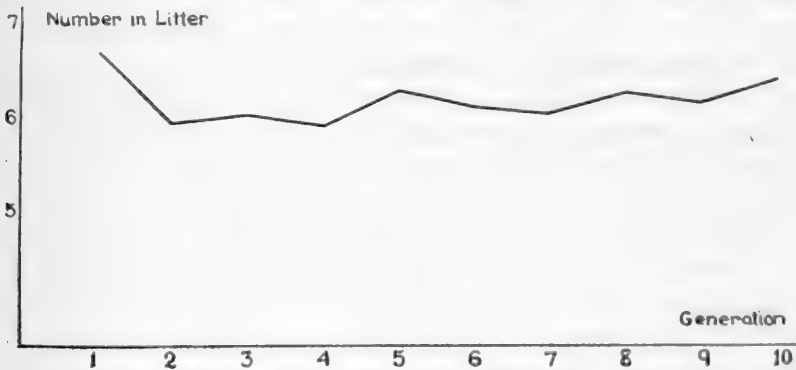


Chart 8 Showing the average size of the litters in different generations of captive Grays.

graph drops to the level that it maintains, with slight fluctuations, until its end.

From the data given above, it is evident that litter production and average litter size in gray rats had not changed appreciably at the end of ten generations of life in captivity. The average number of litters cast by gray females was smaller than the norm for stock albino females, but litter size, on the average, was about the same in the two races.

STERILITY

In commenting on the fact that many wild animals, when brought into captivity, are completely barren or produce but few offspring, Darwin (1875) states that the reproductive

organs of these animals are not diseased, and that the diseases from which they suffer are not those that affect fertility. He shows, furthermore, that this infertility cannot be attributed to failure of the sexual instinct, to a change in climate or in food, nor can it be due to lack of exercise. His conclusion is: "we can in no case precisely say what is the cause of the diminished fertility of an animal when first captured. We can only infer that it is caused by a change of some kind in the natural conditions of life."

The tendency to sterility, which Darwin showed is common to many species of animals when first taken from a state of nature, was exhibited in a marked degree in the case of the wild Norway rats used as foundation stock for our colony of captive Grays. Only six of twenty wild females bore young during the period of their captivity, as far as known. The reproductive power of the females that bred seemed little, if at all, affected by the changed conditions of environment and of nutrition, since the average number of litters they cast and the average size of their litters compared favorably with similar averages for litter production and litter size in later generations (table 7). The fourteen sterile females lived for some months in the colony and appeared to be in good physical condition during this time. Autopsies made on a number of these animals showed no abnormalities or diseases of the reproductive organs, although some of them were found to be suffering from the lung infection which frequently attacks rats of any race after they are a year old. That the changed conditions to which these rats were subjected in some way adversely affected their fertility there can be little doubt.

A factor which may have prevented breeding in many of the wild rats, and one that may be responsible to a greater or a less extent for infertility in other animals when first brought into captivity, was the extreme fear of man which wild rats show in a marked degree. Intense fear produces a nervous tension which undoubtedly influences the activity of many organs of the body, particularly those concerned with secretion. It seems not improbable, therefore, that this nerv-

ous tension, when prolonged, indirectly affects the reproductive organs which are particularly responsive to disturbances of the nervous system. After a time most wild animals become accustomed to life in captivity and they then lose their fear of man to a great extent. With the lessening of nervous tension body organs function more normally. Breeding then takes place at a normal rate, or it is increased in many cases, presumably by the abundant and adequate food that the animals receive and also by the protection from enemies which enables the individuals to live out the normal span of reproductive life.

TABLE 8

Showing sterility in different generations of captive gray rats

GENERATION OF BREEDING FEMALES	TOTAL NUMBER FEMALES REARED	NUMBER FEMALES BREEDING	NUMBER FEMALES STERILE	PER CENT STERILITY
Wild grays	20	6	14	70.00
1	59	37	22	37.29
2	60	42	18	30.00
3	54	44	10	18.52
4	56	50	6	10.71
5	52	46	6	11.54
6	54	48	6	11.11
7	53	48	5	9.43
8	51	48	3	5.88
9	59	48	11	18.64
	518	417	101	19.49

Data given in table 8 show the total number of females reared, the number that did not breed, and the percentage of sterility in each of the nine generations of captive Grays.

As shown in table 8, the sterility in females of the first generation born in captivity was 37.29 per cent, only about half of that (70.00 per cent) in wild females. This percentage is too high, if one takes into consideration the fact that five of the females of the first generation escaped from the colony and were not recaptured. These five females ranged in age from seven to thirteen months at the time of their escape.

None of them had cast young up to this time, but they might have done so later, since many females in the early generations did not breed until they were a year or more old. If these females are omitted from the data in table 8, the sterility for the females of the first generation falls to 31.48 per cent.

The marked decrease in sterility in the offspring of wild females is very significant, since it shows that the majority of them quickly adapted themselves to conditions of life in captivity, which had apparently rendered many of the wild females impotent. Rats of this first generation showed far less fear and less nervous tension than did their wild parents, and all of the females reared their own offspring, which but one of the wild females was able to do.

Sterility decreased steadily as the generations advanced (table 8), and at the fourth generation it had fallen to about 11 per cent, which is the percentage level of sterility in well-cared-for stock Albinos (Slonaker and Card, '23). Sterility reached its lowest point at the eighth generation, where it was but 5.88 per cent. A trend to higher sterility in the stock is not indicated by the increased sterility in the ninth generation. In this generation two of the females died before they were six months old, two others had to be killed because they had ovarian tumors, and three females in one litter developed lung infection at an early age and did not breed although they lived for several months.

The striking decrease in sterility in succeeding generations of these gray rats is shown by the graph in chart 9, constructed from data in table 8.

From the downward trend of the graph in chart 9, it is obvious that the conditions under which these gray rats lived tended to eliminate sterility. In each generation the rats became more adapted to their changed environment, and by the third generation had lost much of their fear of man. They came to the front of the cage when they heard the truck that brought food, and were not frightened when the young were taken out for examination or when the cage was cleaned. The increased fertility in these rats as the generations

advanced can be ascribed, I believe, in part to the lessening of nervous tension, and in part to the fact that the animals were fed on a well-balanced ration containing the elements essential for reproduction.

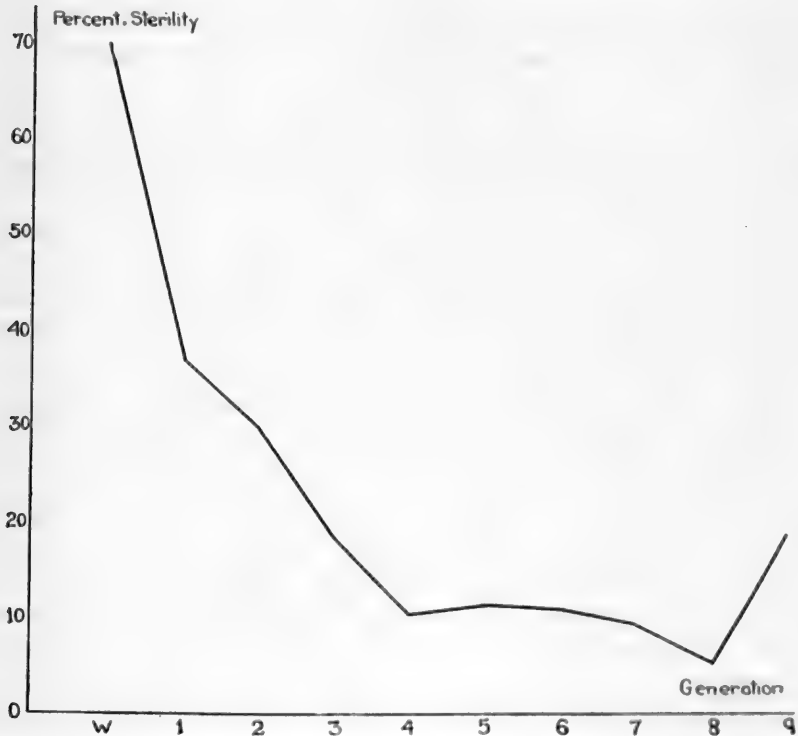


Chart 9 Showing the percentage of sterility in different generations of captive Grays.

Most, if not all, of the sterility found in females of the later generations can be attributed to diseases which affected the reproductive organs or so lowered vitality that the individuals could not breed. Autopsies were not made on rats found dead in the cage, but when it was necessary to kill any individuals because of obvious illness, the fact was noted. Records show that a total of sixteen females belonging in the first nine generations were killed because they had tumors,

chiefly ovarian or mammary. The ear infection, mastoiditis, rendered it necessary to dispose of four other females, while seventeen had to be killed because they had lung disease in an advanced stage.

Some years ago, in collaboration with my colleague, Dr. J. M. Stotsenburg, autopsies were made on a considerable number of albino females, from eight to twenty months old, that had never cast young although they were apparently in good physical condition. These autopsies showed that, in the majority of cases, sterility was due to abnormal or diseased conditions of the reproductive organs. In some females the ovaries were very small and obviously immature; in other females the ovaries were abnormally large, much lobulated, and frequently contained pus; ovarian tumors or cysts were present in other females. A pathological condition of the uterus was the cause of sterility in many cases. In some females the uterus was much congested, the horns containing yellowish nodules of pus; in others the uterus was very small and anemic. An infectious disease of the oviducts, pyosalpinx, was found in some instances. In its early stages lung infection does not prevent conception, but it seriously interferes with embryonic development. Offspring of infected mothers are usually very small at birth, many of them are born dead, and those that live show low vitality and usually die at an early age. As this disease advances, it leads to complete sterility. It seems probable that infertility in female rats is due chiefly to diseases affecting the reproductive organs or to the devitalizing effects of lung infection. Impotency in males is comparatively rare, and when found is caused mainly by diseases, such as lung infection, that lower the vitality of the individuals.

As previously stated, if gray females were in good physical condition they were kept until it was evident that breeding was at an end. Autopsies made on old females that had not cast young for several months frequently showed that a state of pregnancy existed, but that the embryos were in the process of being resorbed. It is evident, from this finding, that ovula-

tion takes place when females are relatively old, and that the ova liberated are capable of being fertilized, but that senescence has produced changes in the uterus that render it impossible for the embryos to undergo normal development. These changes evidently occur at various ages in different individuals, which accounts for the curtailing or the lengthening of the reproductive period, but what they are and how they interfere with embryonic development remains to be determined.

Data given in this section show that sterility in captive gray females had decreased from 70.00 per cent to less than 10 per cent at the end of nine generations. The cause of this decrease can probably be attributed largely to a lessening of nervous tension as the animals became more adapted to changed conditions of environment and to the adequate food that they received. Infertility in females of the later generations was due chiefly to diseases that affected the reproductive organs or to decreased vitality resulting from lung infection.

THE SEX RATIO

The proportion of the sexes at birth in wild Norway rats has not been determined as yet. Data obtained by Miller ('11) showed that there were twenty-three males and twenty-eight females, or a sex ratio of 82.1 males to 100 females, in five litters cast by caged females of unknown ages. Among trapped animals, according to Lantz ('09) and Donaldson ('12), males are in excess, as a rule. This finding does not indicate the relative proportion of the sexes among adult animals generally, however, since the females, if suckling young, probably remain in or close to the nest most of the time and therefore are not as readily trapped as are the males. Sex ratios for gray Norway rats, given in previous publications (King, '24, '27) were based on data obtained from the series of these animals that form the material for the present study.

The sex distribution and the sex ratio in the entire series of 1539 litters comprised in the first ten generations of captive Grays are given in table 9.

As shown in table 9, litters forming the first generation of captive gray rats, which were cast by wild females of unknown ages, contained a total of 139 young, among which the sexes were very evenly distributed, the ratio being 98.57 males to 100 females. In the second generation the ratio dropped to 81.95 males to 100 females. The difference of 16.62 ± 11.94 between the ratios for the first and second gen-

TABLE 9

Showing sex distribution and sex ratio in different generations of captive gray rats

GENERATION	TOTAL NUMBER INDIVIDUALS	MALES	FEMALES	NUMBER MALES TO 100 FEMALES
1	139	69	70	98.57 ± 11.37
2	857	386	471	81.95 ± 3.79
3	691	319	372	85.75 ± 4.41
4	849	418	431	97.18 ± 4.49
5	1202	611	591	103.38 ± 4.02
6	1084	553	531	104.14 ± 4.26
7	1167	570	597	95.47 ± 3.78
8	1063	530	533	99.43 ± 4.11
9	1293	653	640	102.03 ± 3.82
10	1160	571	589	96.94 ± 3.84
	9505	4680	4825	96.99 ± 1.34

erations is considerable, but it cannot be deemed as statistically important because of the size of its probable error. In succeeding generations the sex ratio rose gradually, reaching its maximum, 104.14 males to 100 females, in the sixth generation, after which it declined slightly.

The changes in the sex ratio with the advance of the generations are shown graphically in chart 10.

Aside from its sharp decline at the second generation, the graph in chart 10 shows only minor fluctuations and tends to run at a level which indicates a nearly equal proportion of the sexes.

In the entire series of 9505 individuals the sex ratio was slightly under equality, being 96.99 ± 1.34 . Deviations from this ratio in any generation are not great enough to be considered as significant.

If it is assumed that the sex ratio found in the young of the first generation is about that normal for the race in its wild state, it follows that changed conditions of life in captivity must have influenced the proportion of the sexes in the two succeeding generations, since the sex ratios in these generations were relatively low. Males are seemingly less viable

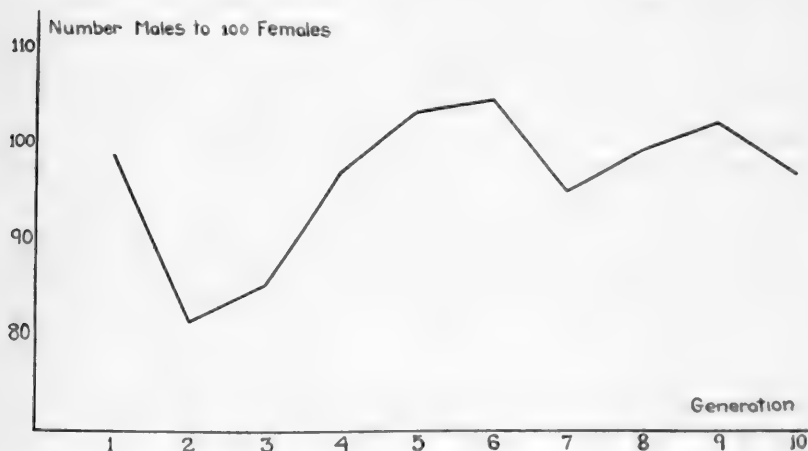


Chart 10 Showing the sex ratio in different generations of captive gray rats.

than females at all stages of development, and their mortality at birth and during early postnatal life is greater than that among females (King, '15). The most obvious explanation, therefore, for the drop in the sex ratio at the second generation is that change in environment rendered fetal mortality selective, and that it bore more heavily on male than on female embryos.

There is, however, another factor which may have affected the sex ratio in the early generations of these rats. It has been shown in a previous publication (King, '24), and the finding confirmed by a large series of data obtained more

recently, that in the albino race the age of the mother has a pronounced influence on the sex ratio in her young. In general, when the data for litters cast by a considerable number of females are examined, it is found that males tend to predominate in litters cast by young mothers and by those that are from ten to fourteen months old, and that female young are in excess, as a rule, in litters produced when the mothers are at the height of their reproductive activity (from six to nine months of age) and when they are approaching the menopause. In what manner the age of the mother can affect the sex proportions in the young is unknown. It may be that changes occur in the uterus at different age periods that tend to favor the development of embryos of one sex rather than those of the other, or there may be age changes in the amount or in the nature of various hormones that at one time render the ova more readily fertilized by spermatozoa that are male-producing and at another time favor fertilization by spermatozoa that are female-producing. Whatever these changes are, they tend to balance each other in the long run. When a female breeds at a normal rate throughout reproductive life, the sex ratio in the entire number of offspring is usually near equality, unless disturbing factors, such as hybridization, produce alterations in the ratio at all periods during the reproductive life of the mother.

As shown in a previous section of this paper, gray females of the early generations began breeding at an average age of about eight months (table 6). At this age albino females are at the height of their reproductive power and their litters contain, as a rule, an increased number of female young. Conditions of captivity, seemingly, eliminated in the gray rats the early period of breeding which seems to favor the development of male young. The reproductive life of these females, therefore, comprised two periods when female young tend to predominate in the litters cast, and but one period when male young tend to be in excess. Their litters, as shown in table 9, contained a greater proportion of female than of male young. As the generations advanced, an increasing

number of females began breeding at an earlier age. The reproductive life of these females included all four periods in which the sex ratio tends to change with the age of the mother. In the young born to these females the sex ratio was near equality (table 9).

Changed conditions of life in captivity apparently had no direct effect on the sex ratio in the litters cast by gray females. They may be considered to have influenced the ratio indirectly, however, by first shortening and then lengthening the average span of reproductive life in the females. From the evidence given it seems more probable that the variations in the sex ratio found in the different generations of these rats can be ascribed to physiological changes due to the advancing age of the mothers rather than to differential mortality during fetal life.

MORTALITY

The scope of this study did not include a determination of the normal duration of life in captive gray rats, as it seemed more important to ascertain the condition of the central nervous system and of various other organs before they had been seriously affected by senescence or by disease. Most of the rats, therefore, were killed and dissected when they reached the age of twenty months. Data regarding the mortality at various age periods and the chief causes of death are given in the present section.

In the entire series of 9505 young born in the first ten generations, only eighteen individuals, ten males and eight females, were found dead at birth. The mortality at this time, about 0.19 per cent, was therefore very low, and much less than that usually found in stock Albinos, where the still-born form about 2 per cent of all the offspring cast (King, '21). Since all of the litters could not be examined at the time of birth, there is the possibility that the number of stillborn was greater than the records show and that such individuals were eaten by the mothers.

The mortality among the young during the suckling period was considerable, as the mothers frequently destroyed or neglected their young if the nest was disturbed or the young removed for examination. Mortality among the young at this period was still further increased by the fact that the adults in the cage usually crowded into the nest when frightened, and in consequence some of the young were often crushed or suffocated. As the young rats were able to look out for themselves after their eyes were opened, at the seventeenth day of postnatal life, the mortality among them from this time until the end of the suckling period at thirty days was negligible. Litters finally selected for weighing and as parents of the succeeding generation were those in which there were no deaths until the animals had passed the age of sixty days.

Table 10 shows, for each generation, the number of individuals of each sex living at the age of twelve months, the time when reproductive activity has passed its height and the animals have not yet become seriously affected by lung disease. This table also gives the number of animals still living at twenty months of age, together with the percentages of mortality that had occurred at the two ages specified. A summary of the data by generation groups is also included.

In all generations, as the data in table 10 show, mortality was very low during the first year of life, averaging less than 4 per cent in both sexes. Deaths during this period were due, in the main, to accident or to the savageness of some of the rats that caused them to kill other individuals in the cage.

The mortality increased greatly after the rats were a year old, being due chiefly to lung infection. In the first generation 80 per cent of the individuals of both sexes died before reaching the age of twenty months. The high mortality among the older rats of this generation was probably due, in part, to lack of adjustment to conditions of captivity which rendered them very susceptible to disease.

The change in mortality with the advance of the generations is shown in the lower part of table 10, where the data

for the second to the tenth generations are combined in groups of three generations. In the males of the first group (second to fourth generations) the mortality at twelve months was 5 per cent, which was about twice as great as that in the second group (fifth to seventh generations). The mortality in the third group of males (eighth to tenth generations) was 0.6 per cent higher than that in the second group.

TABLE 10
Showing mortality in different generations of captive gray rats

GENERATION	MALES					FEMALES				
	Number individuals	Number living at 12 months	Number living at 20 months	Per cent mortality at 12 months	Per cent mortality at 20 months	Number individuals	Number living at 12 months	Number living at 20 months	Per cent mortality at 12 months	Per cent mortality at 20 months
1	50	48	10	4.0	80.0	52	49	10	5.8	80.8
2	54	50	37	7.4	31.5	60	55	28	8.3	53.3
3	53	53	23	0.0	56.6	54	52	29	3.7	46.3
4	52	48	29	7.7	44.2	55	55	33	0.0	40.0
5	54	52	38	3.7	29.6	52	48	35	7.7	32.7
6	53	51	40	3.8	24.5	54	52	34	3.7	36.6
7	50	50	35	0.0	30.0	53	53	40	0.0	24.5
8	52	50	34	3.8	34.6	51	49	38	3.9	25.5
9	53	52	41	1.9	22.6	59	57	50	3.2	15.3
10	50	48	34	4.0	32.0	52	51	42	1.9	19.2
	521	502	321	3.6	38.4	542	521	339	3.9	37.4
2-4	159	151	89	5.0	44.0	169	162	90	4.1	46.7
5-7	157	153	113	2.6	28.0	159	153	109	3.8	31.4
8-10	155	150	109	3.2	29.7	162	157	130	3.1	19.8

In the females, at twelve months, the change in mortality as the generations advanced was relatively slight, falling from 4.1 to 3.1 per cent from the first to the third group.

The mortality at twenty months for males of the first group was 44 per cent, and it dropped subsequently about 14 per cent. In the females at this age the mortality showed a marked decrease as the generations advanced, being 26.9 per cent less in the third than in the first group. From these findings it is evident that conditions of captivity tended to

lengthen the average span of life in these gray rats, since at both twelve and at twenty months of age the mortality was less in individuals of the later generations than in those of the earlier generations.

Data given in table 10 show that there was practically no difference in the mortality of males and of females in the series as a whole. In both sexes, at twelve months, the mortality was about 4 per cent; at twenty months it was about 38 per cent. The mortality in males and females of the different generations at twenty months is shown by graphs in chart 11 constructed from data in table 10.

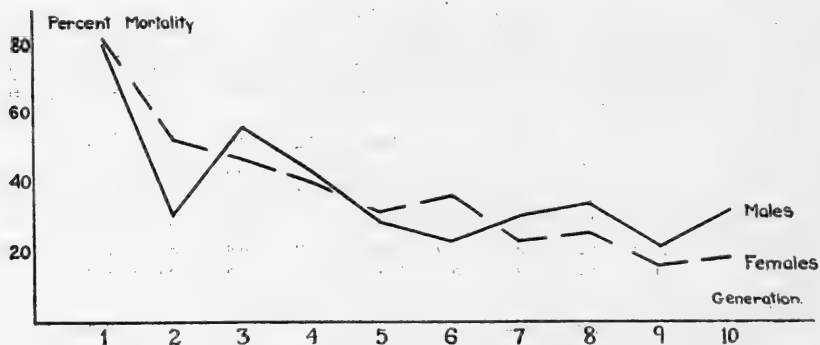


Chart 11 Showing the percentage of mortality at twenty months in males and females of the different generations of captive Grays.

In chart 11 the graph for the females starts slightly higher than that for males, but drops below at the third generation. Subsequently the graphs cross and recross, but after the sixth generation the graph for females runs below that for males until the end of its course. In the later generations, therefore, the mortality was less in females than in males.

Such data as have been obtained indicate that males are less viable than females at birth and during early postnatal life. During adolescence and early maturity there is apparently little difference in the mortality of the two sexes. In later life, however, mortality among males again seems to be greater than that among females. Lung disease, which

is responsible for the majority of deaths among older rats, is seemingly more common in males than in females. On the other hand, cancer and tumors are far more prevalent in females than in males. In the first ten generations of gray rats eighteen females and only one male were killed because of such growths. A third ailment, frequently found in rat colonies, is the middle-ear infection which produces disequilibrium and circular movements (Donaldson, '24). Only six cases of this disease were found in the gray rats. The affected individuals were killed as soon as they showed the characteristic symptoms of the disease, as the infection is readily transmitted to other individuals in the cage.

From the findings recorded in this section it appears that in the first ten generations of captive gray rats mortality was very low at birth. It increased during the suckling period, but fell during adolescence and early maturity. After the animals reached the age of one year the death rate rose considerably. As the generations advanced, the mortality at twelve and at twenty months of age decreased in both sexes, but among the older individuals the decrease was more marked in females than in males. The chief causes of death were lung disease and malignant growths.

BEHAVIOR

Since little is known of the general behavior of gray rats living in their natural habitat, it seems worth while to record here the outstanding traits of the wild animals which were brought into the colony to start the strain of captive Grays, and to note the changes in these traits that occurred as the animals became adjusted to their new environment.

When first captured, wild rats were much frightened and so appeared very savage and vicious. They were constantly in a state of high nervous tension due, apparently, to an instinctive fear of man and to the restriction of their activity that captivity imposed. If the cage was approached they began running about, fighting and screaming in obvious terror. When they had been exhausted by such efforts, they

huddled together in a corner of the cage, trembling and clicking their teeth incessantly, or they tried to hide under the bedding material. If the cage door was opened they were apt to jump directly at one's face in a frantic effort to escape. Food put into the cage, no matter how hungry the rats might be, was never touched until the workers in the colony had departed for the day. These rats were very quarrelsome, and some of them were killed and eaten by the more powerful individuals.

The wooden cages that housed these rats had to be protected at all vulnerable points with heavy wire or iron sheeting, as the rats were constantly seeking a way to escape. If they succeeded in loosening the protective covering at any point they would gnaw a large hole through the thick wood of the cage in a few hours. When trapped after such an escape they showed excessive fright for a considerable time. It was several months before these rats became sufficiently accustomed to their new environment to render the work of caring for them and of taking necessary records other than an arduous task.

Miller ('11) has given an account of the mating behavior of gray rats in captivity that is in accord with my own observations. This subject, therefore, need not be considered here. Miller also noted the fact that wild gray females are prone to kill and devour their young at or shortly after birth—a tendency which led to the destruction of a number of litters in our colony also. As already stated, it became necessary to remove the young of the first generation from the cage as soon as they were discovered and to give them to an albino female to rear in order to obtain any litters with which to start the strain.

Since it would have been of distinct advantage in working with these rats of the first generation to have them tame enough to be handled without the use of ether or of forceps, as are albino rats, an attempt was made to tame some of the young that were suckled by albino foster mothers. After the rats were a week old they were taken from the nest each

day and handled gently for a time. They submitted to this handling without much protest until their eyes were opened. After this time they began to bite when held, and they were so frightened and so nervous that the idea of taming them was abandoned. Two young rats of the third generation, a male and female, were taken in charge by an assistant, Miss Ruth Meeser. She succeeded in taming them so that she could handle them at will throughout their lives. They were always very nervous, however, and would not submit to being held by any one who was not a constant worker in the colony.

Females of the first, and those of subsequent generations, reared their own young. It was necessary to wear gloves when the young of the early generations were removed from the nest for examination. If the young were returned to the mother with human odor clinging to them she frequently killed them at once or refused to care for them. In later generations the females did not show much concern if the nest was disturbed and the young handled with bare hands. When they were returned to her, however, she usually carried them to a corner of the cage and built a new nest.

As the generations advanced, the rats gradually lost much of their savageness as well as their fear of man. By the fifth generation they were sufficiently tame to remain quietly in the corner of the cage when the door was opened or the cage cleaned. They came to the front of the cage, as do Albinos, when they heard the sound of the truck that brought food and began eating as soon as food was available. Many of them would take bits of food pushed through the wire of the door, if offered by some one to whom they were accustomed. They were, however, always alarmed at the approach of strangers and promptly went in hiding. Evidently they could distinguish between colony workers and strangers through their keen sense of smell.

It has been the custom, throughout the course of this experiment, to place males of one litter with females of another litter when the young are removed from the mother at the time of weaning. These rats, therefore, grow up together

and they are usually kept together throughout life. Occasionally, for some reason as yet unknown, one of the males in a cage will grow much faster and become considerably larger than its brothers. When this male is powerful enough it dominates the 'home.' The other males are not permitted to mate with the females, as a rule, and they are forced to stay in a corner of the cage away from the nest. Sometimes this dominant male becomes very vicious and develops 'killer' instincts. He then either kills the other males or injures them so severely that they have to be removed from the cage; females are rarely molested in any way. It would appear probable, from this finding, that in a state of nature gray rats are inclined to be polygamous, the most vigorous male driving out or killing the other males and then occupying the burrow with several females. Such a condition exists in many other wild species, as is well known.

Occasionally a female that has become larger than her sisters will exhibit the 'killer' traits shown by males. One such female, weighing over 400 grams, killed two sisters and two males in the cage. She lived peacefully for some months with the remaining male that was considerably larger than herself, and took very good care of her numerous offspring as long as they remained with her.

A most pronounced characteristic of gray rats, and one that time and captivity have not changed to any extent as yet, is their decided aversion to the presence of strange rats. If the inhabitants of the cage are adults, they will at once attack and soon kill the intruder, no matter how large it may be. Even if the new arrival had formerly been housed in the cage, and had been absent but a day or two, it promptly meets with the same fate as that of a total stranger. When a rearrangement of adult rats of mixed sexes is necessary, the only way to insure each of the individuals more than a fair chance of life is to etherize all of the rats, give them a bath in a fairly strong solution of some disinfectant, such as creolin or larkspur, and then place them in a recently sterilized cage containing a quantity of sterilized bedding. The

bath destroys the nest odor of the rats and sterilization removes all other animal odors from the cage and bedding. The rats huddle together under the bedding for some time, dazed by the ether and thoroughly cowed by the treatment they have received. When they have become dry and have ventured from hiding to inspect their new quarters, they are usually friendly and do not fight subsequently. Even this drastic treatment is not always effective, however, and after this procedure it is not uncommon to find on the following day that one or more of the individuals have been killed.

By the end of ten generations in captivity, the behavior of these gray rats had changed considerably in many respects: they had lost much of their viciousness and their fear of man; females rarely killed the young returned to the nest after being handled with bare hands; their nervous tension was distinctly less than that in animals of the earlier generations, although they were obviously frightened when taken from the cage to be weighed or when the cage was approached by those to whom they were not accustomed; they made but little effort to escape when the door of the cage was opened or when the cage was cleaned. Rats of the later generations had not, however, overcome their aversion to the presence of strange individuals, and such intruders were killed as promptly as in the earlier generations.

Although gray rats of the later generations were somewhat more nervous and more easily frightened than are the general run of Albinos, they were far more vigorous and active, and they tended to be larger animals, especially the females. Sterility in these Grays was much less than that commonly found in stock Albinos, and the two races were nearly equal as regards fertility. The life span in the Grays compared very favorably with that in the Albinos, and both races showed about the same susceptibility to lung infection and to other diseases. Because of their size and vigor, these Grays would seem to be superior to Albinos for many laboratory purposes. When captivity has rendered them tame enough to be handled easily, they should be valuable material

for experimental work requiring a pure strain of known ancestry.

SUMMARY

1. The analysis of various life processes in captive gray rats, as given in part I of the present paper, is based on data for the first ten generations of these animals that descended from six wild Norway females brought into The Wistar Institute Animal Colony in the spring of 1919. Data given comprise 1539 litters, containing 9505 individuals, 4680 males and 4825 females.

2. Marked changes in the rate and in the extent of body growth occurred in both sexes of captive Grays as the generations advanced (tables 1 to 3). At the tenth generation growth during early life was much more rapid than that in animals of the first generation, and was approaching the albino type. Growth during adult life changed relatively little, however, as the average body weight of adult males in the tenth generation was only about 4 per cent greater than that of males in the first generation (table 4, chart 4); in adult females the body weight had increased about 8 per cent (table 4, chart 5).

3. The variability in body weight at birth was about the same in both sexes of captive Grays, but the range of variation in the birth weights was slightly greater in males than in females.

4. Males of the tenth generation were significantly less variable in body weight throughout adult life, but not during early life, than were males of the first generation (table 4); females of this generation showed a slight decrease in variability at all age periods (table 5).

5. As the generations advanced, the trend of variability in both sexes of captive Grays was toward that found in stock Albinos. Males of the tenth generation were slightly more variable in body weight during early life than were females, but a reverse relation was found throughout adult life (tables 4 and 5). In both sexes variability in body weight was cor-

related with the growth rate, as is the case in the albino rat and in man.

6. Evidence presented indicates that variability in the body weight of rats during postnatal life is due, in part, to differences in the genetic constitution of the individuals.

7. The average age at which females of the early generations cast their first litters was seven months. With the advance of the generations breeding began at an earlier age; consequently, the average length of the reproductive period was increased by about two months (table 6, chart 7).

8. The average number of litters cast by gray females of the first nine generations was 3.69. Deviations from this mean in any generation were too small to be significant (table 7).

9. The range in litter size was from one to fourteen, with the average 6.1. This average had not changed appreciably at the end of ten generations (table 7, chart 8).

10. Sterility was very high (70 per cent) in the wild females which formed the foundation stock for this series of captive Grays. It decreased steadily, however, as the generations advanced, falling to 5.88 per cent at the eighth generation (table 8, chart 9). Sterility was due chiefly to diseases affecting the reproductive organs or to decreased vitality resulting from lung infection.

11. In the entire series of individuals the sex ratio was 96.99 ± 1.34 . Deviations from this ratio in any generation were not statistically important, and they are ascribed, tentatively, to physiological changes due to the advancing age of the mothers rather than to differential mortality during fetal life.

12. Mortality at birth was very low in the first ten generations of captive Grays (0.19 per cent). It increased during the suckling period, fell to a low point during adolescence and early maturity, and showed a marked rise after the animals were a year old.

13. In the series as a whole the mortality was about the same in the two sexes at the age periods noted, being about

4 per cent at the age period of twelve months and 38 per cent at the age period of twenty months (table 10). In the later generations the mortality at twenty months tended to be less in females than in males (chart 11).

14. Mortality decreased steadily as the generations advanced. In males it fell from 80 per cent in the first generation to 32 per cent in the tenth generation; in females the drop was from 80 per cent to 19 per cent. The chief causes of death were lung disease and malignant growths.

15. Marked changes in behavior occurred during the course of ten generations. The rats gradually lost much of their savageness as well as their fear of man, and their nervous tension decreased considerably.

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PART II, SERIES 1. OBSERVATIONS ON THE BODY MEASUREMENTS AND ON THE WEIGHTS OF SOME ORGANS OF CAPTIVE GRAY NORWAY RATS

HENRY H. DONALDSON

MATERIAL AND PROCEDURE

The rats examined were all bred and reared by Doctor King. For this study, series 1, 499 animals have been dissected according to a uniform method by Miss Ruth Meeser. It was planned to use about twenty rats of each sex in each generation, but, as the tables 1 and 2 show, this number has, on the average, been slightly exceeded.

In each case the body length and body weight were determined. The organs weighed were the brain and two of its parts: the olfactory bulbs and the paraflocculi; also the hypophysis, the thyroid, the suprarenals, and the gonads. To interpret these data the values observed for each case were referred to the corresponding values for either the wild gray Norway or the albino rat taken from a series of tables found in *The Rat* (Donaldson, '24), and the deviations from these standards determined. In the text that follows, these tables are distinguished by the numbers which they bear in the publication just noted and the citations are in italics. Since the effort is here being made to follow not only the way in which the gray Norway rat in captivity departs from the Albino, but also from the wild strain, in respect of the characters studied, it would have been ideal could we have had also a complete series of reference tables for the wild Norway to be used for every comparison. Such reference data, however, are available only for the body length, body weight, and the brain weight. For the other comparisons with the wild strain, it has been necessary to use a series of short tables

compiled by Hatai ('14) giving the weights of the several organs in the wild strain. Taken altogether, these tables indicate the values for the several organs in the wild strain and give a basis for determining the changes shown by the captive Grays.

For conciseness we shall use, in the subsequent text, the term 'captive Grays' for the Norway rats here considered.

In forming the tables and charts that follow, the procedure has been this: The datum for any organ or part of an individual captive Gray is compared with the corresponding datum from the appropriate reference table, the comparison being based either on the observed body weight or body length. Using the datum in the reference table employed as the standard, the percentage deviation, plus or minus, of the observed values for the captive Grays has been determined. The average of all the individual variations in one sex group of a given generation is the datum entered in the condensed tables here presented.²

The deviations based on the observed body weight and on the observed body length are both given in the tables. As will be shown later, however, the body weight exhibits a relative increase between G_1 and G_{10} , and for this reason only the deviations based on body length are used for the graphs in the charts. In tables 11 and 12 there are given for each sex of each generation the average ages and the average body lengths, but these data are not repeated in the later tables. In the charts the reference-tables values are represented by the base line and the percentage deviations of the captive Grays are entered in their proper relations to this. The same base line, of course, represents the reference values for both males and females. Any departures from this general arrangement of the tables or charts will be noted as they occur.

BODY LENGTH

The values for the mean body length as given in tables 11 and 12 are entered in chart 12. The fluctuations in the graphs

² The individual data are on file at The Wistar Institute, where they may be consulted.

for both sexes have the same trend, except at G_{10} . Between G_3 and G_{10} the maximum difference is about 6 per cent in both sexes.

At G_1 the age of the group is high and at G_2 it is low in both sexes as compared with the subsequent age values. As would be expected, the older group, G_1 , has a greater length and the younger, G_2 , a lesser length. There is a markedly low length at G_5 , and, as later observations will show, this is probably a retardation in growth in response to unfavorable conditions acting on this generation. As the data stand, there is no significant difference at 600 days between the body length at G_3 and at G_{10} , so that there is no evidence that the captive Grays have undergone a progressive change in body length on age during this period.

TABLE 11

General data on the number, age, body length, and body weight of the gray Norway rats used for this study and the deviations of the observed body weight from the body weight as given in the reference table 187 (The Rat, '24) for the observed body length. Charts 12 and 13. Males

GENERATION	NUMBER OF CASES	AVERAGE AGE IN DAYS	BODY LENGTH OBSERVED	BODY WEIGHT OBSERVED	BODY WEIGHT ON BODY LENGTH OBSERVED (TABLE 187)	DEVIATION OF OBSERVED BODY WEIGHT
			<i>Mm.</i>	<i>Grams</i>		<i>Per cent</i>
Wild	4		188	174	146	+ 16.0
G_1	23	726	241	352	335	+ 4.8
G_2	43	533	234	331	301	+ 9.0
G_3	18	600	240	380	330	+ 13.1
G_4	27	602	249	404	378	+ 6.4
G_5	20	607	235	346	306	+ 11.5
G_6	20	600	247	390	367	+ 5.9
G_7	23	595	246	393	361	+ 8.1
G_8	21	602	237	359	315	+ 12.2
G_9	20	606	236	383	310	+ 19.0
G_{10}	20	606	238	384	320	+ 16.6

TABLE 12

General data on the number, age, body length, and body weight of the gray Norway rats used for this study and the deviations of the observed body weight from the body weight as given in the reference table 187 (*The Rat*, '24) for the observed body length. Charts 12 and 13. Females

GENERATION	NUMBER OF CASES	AVERAGE AGE IN DAYS	BODY LENGTH OBSERVED	BODY WEIGHT OBSERVED	BODY WEIGHT ON BODY LENGTH OBSERVED (TABLE 187)	DEVIATION OF OBSERVED BODY WEIGHT
			<i>Mm.</i>	<i>Grams</i>		<i>Per cent</i>
Wild	6		200	184	182	+ 1.1
G ₁	18	704	225	275	270	+ 1.8
G ₂	26	578	216	256	234	+ 8.6
G ₃	26	589	221	269	253	+ 5.9
G ₄	24	605	225	265	262	+ 1.1
G ₅	18	608	220	276	249	+ 9.8
G ₆	18	597	232	326	300	+ 7.9
G ₇	21	596	225	287	270	+ 5.9
G ₈	22	596	225	304	270	+ 11.1
G ₉	20	605	224	308	265	+ 13.9
G ₁₀	21	607	221	302	253	+ 16.2

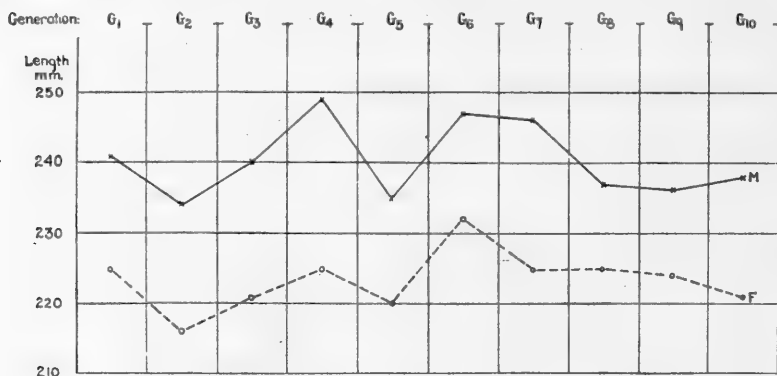


Chart 12 Body length in millimeters. —, male; ----, female.

BODY WEIGHT—ON OBSERVED BODY LENGTH—STANDARD: WILD GRAY NORWAY. *Reference table 187*

When the data in the last columns of tables 11 and 12 are plotted in chart 13, it is seen that the body weight of the captive Grays tends to increase from G₁ to G₁₀. The two sexes behave in a similar manner, though the male is a trifle more

responsive, and at G_{10} the body weight of the captive Grays exceeds that of the wild strain by 17 per cent in the males and by 16 per cent in the females.

If data for the wild gray Norway, taken from *reference table 187*, are compared with data for the Albino, taken from *reference table 144*, using the body lengths that belong to each sex of the captive Grays, it appears that at G_{10} the body weight of the Albino exceeds that of the wild gray Norway by 15 per cent in the male and by 19 per cent in the female.

Thus, the deviation in the body weight of the captive Grays from that of the wild gray Norways is similar to the deviation shown by the Albino. The captive Grays have, therefore, approximated the Albino in this relation. It seems most probable that lack of exercise and the supply of abundant food are the influences which have brought about this modification.

Attention should be called at this point to the sag in the graphs in chart 13, at G_6 and G_7 . A corresponding sag occurs in the graphs for most of the other organs, and in the present instance is to be explained as the result of unfavorable conditions acting on these generations (chart 1).

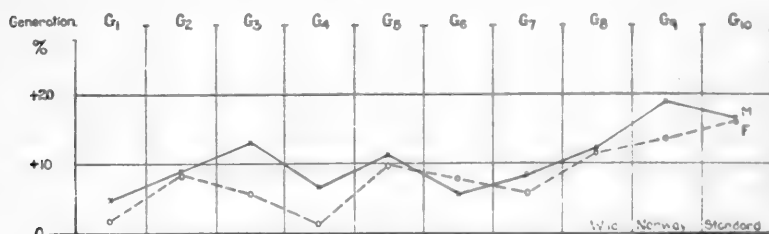


Chart 13 Deviations of observed body weight from standard body weight on observed body length. Standard: Wild Norway, table 187.

ON THE WEIGHTS OF THE SEVERAL ORGANS IN THE CAPTIVE GRAYS

Introduction

There are two ends in view. In the first place, it is the purpose of this study to determine whether the captive Grays have departed from the standards for the wild strain.

For this purpose the observed data are compared with those for the brain, *reference table 187*, or with those for the other organs of the wild Norway in the tables from Hatai ('14).³ These latter are partial tables only, but can, nevertheless, be used for our present purpose. Such comparisons show how the data for the captive Grays differ from those for the wild strain.

In the second place, we wish to determine how the data for the captive Grays are related to those of the Albinos. To do this the data in the several reference tables for the Albino are used as standards, and the deviations of the observed values similarly determined.

In the tables giving the data on the organ weights there are entered the percentage deviations of the observed from the standard values on both the body weight and body length, as observed. In the charts, however, the graphs for the deviations based on body lengths are alone given.

There are no reference tables for the weights of the olfactory bulbs or of the paraflocculi, and the observations on these parts of the brain have, therefore, been presented from the standpoint of their relation to the observed weight of the entire brain. In the case of the hypophysis, this relation has also been shown.

ON THE WEIGHT OF THE BRAIN AND OF SOME OF ITS PARTS

Standard: Data in *reference table 187* for the wild gray Norway. In the wild gray Norway the brain is heavier than in the Albino.

In tables 13 and 14 the weight of the brain in the successive generations is given for each sex and also the percentage deviations from the standard values. No tables are given for the limiting values in each generation, as shown in charts 15 and 16. In table 15 are given the weights of the olfactory bulbs and of the paraflocculi and the percentage values of the

³ For convenience, the tables from Hatai ('14) are cited under the numbers which designate them in *The Rat* (Donaldson, '24).

brain weight represented by them. The data for these parts do not begin until G_3 .

In chart 14 the percentage deviations of the brain weight are entered and also the percentage of the weight of the brain represented by the olfactory bulbs and by the paraflocculi. In charts 15 and 16 the limiting values for the deviations in brain weight are shown for each generation. Examination of chart 14 shows that the brain weight in the captive Grays is slightly deficient, but with fluctuations.

These deficiencies tend to follow the same course in the two sexes, but are slightly greater in the males, and in both sexes slightly greater in the last five generations, even when the entries at G_7 and G_8 , which mark a sag in the graph, are excluded.

TABLE 13

On the weight of the brain in the captive Grays and on the deviations from the corresponding standards for body weight and body length. Chart 14. Males

GENERATION	NUMBER OF CASES	BRAIN WEIGHT				
		Observed	Standard on body weight observed	Standard on body length observed ¹	Percentage deviation from standard	
					On body weight	On body length
		<i>Grams</i>	<i>Grams</i>	<i>Grams</i>		
G_1	23	2.190	2.342	2.337	—6.5	—6.3
G_2	43	2.138	2.284	2.267	—6.4	—5.7
G_3	18	2.237	2.363	2.329	—5.3	—4.0
G_4	27	2.317	2.380	2.378	—2.7	—2.6
G_5	20	2.198	2.338	2.301	—6.0	—4.5
G_6	20	2.255	2.376	2.364	—5.1	—4.6
G_7	23	2.182	2.379	2.361	—8.3	—7.6
G_8	21	2.150	2.356	2.312	—8.7	—7.0
G_9	20	2.196	2.379	2.305	—7.7	—4.7
G_{10}	20	2.205	2.374	2.320	—7.1	—4.9
					Average:	—5.2

¹As the values for the brain weight on observed body length are averages for the values in table 187 for the brain weight on the body length of each individual case, and as this assumes that the graph between the extremes is a straight line, which it is not, these averages differ slightly, by tenths of a per cent, from the values to be expected for the average body lengths that have been used. This deviation is neglected. The same comment applies to the other organ values in the several tables.

TABLE 14

On the weight of the brain in the captive Grays and on the deviations from the corresponding standards for body weight and body length.

(Chart 14.) Females

GENERATION	NUMBER OF CASES	BRAIN WEIGHT				
		Observed	Standard on body weight	Standard on body length	Percentage deviation from standard	
					On body weight	On body length
		<i>Grams</i>	<i>Grams</i>	<i>Grams</i>		
G ₁	18	2.105	2.213	2.207	— 5.1	— 4.9
G ₂	26	2.124	2.188	2.161	— 2.9	— 1.8
G ₃	26	2.094	2.206	2.192	— 5.1	— 4.5
G ₄	24	2.146	2.199	2.208	— 2.4	— 2.8
G ₅	18	2.093	2.209	2.179	— 5.3	— 4.0
G ₆	18	2.172	2.273	2.249	— 4.4	— 3.4
G ₇	21	2.072	2.229	2.208	— 7.1	— 6.2
G ₈	22	2.069	2.250	2.210	— 8.0	— 6.4
G ₉	20	2.105	2.258	2.209	— 6.8	— 4.7
G ₁₀	21	2.139	2.248	2.192	— 4.9	— 2.4
					Average: — 4.1	

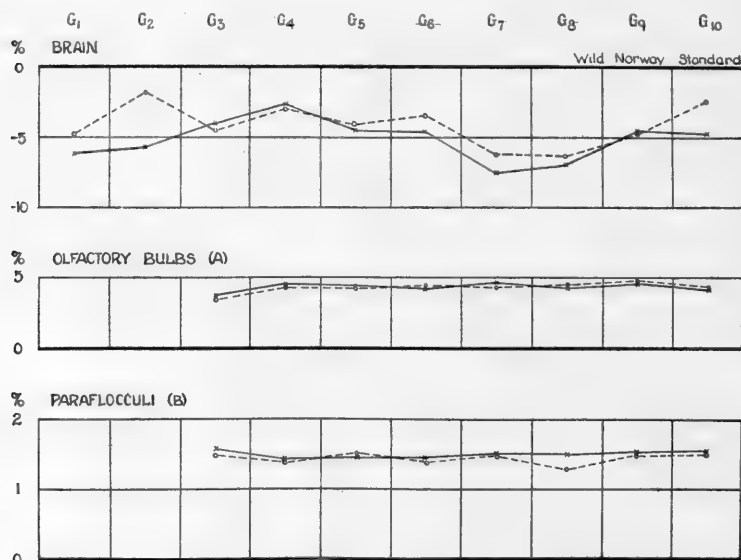


Chart 14 Brain weight—deviations on body length. Standard: Table 187 for wild Norway. —, male; ---, female.

Chart 14 a Percentage weights of olfactory bulbs on brain weight.

Chart 14 b Percentage weights of paraflocculi on brain weight.

The captive Grays show, therefore, a slightly smaller brain weight than the wild strain, but the terminal values at G_{10} are, if anything, a little above those at G_1 , so that there is no evidence of a progressive decrease in brain weight in the successive generations. The low values at G_7 and G_8 are considered as due to the unfavorable conditions in the colony which acted on these generations during the early phases of their development. It will not have escaped notice that the weight of the brain in the original ancestors of the captive Grays has not been considered. The data which we have indicate a brain weight about that of the standard in the male and some 3 per cent below the standard in the female, but the number of cases is too small to give anything satisfactory in the way of an average. The data suggest that there was a sudden drop in the brain weight at G_1 . What this means, if it occurs, is not at the moment clear.

In view of the paucity of the data for the ancestors, the deviations which may occur between them and the G_1 generation are not considered in the discussion that follows, and any changes which are recorded are referred to G_1 as the starting-point.

The slightness of the reduction in the brain weight of the captive Grays was a surprise, as a much greater reduction had been expected. This expectation was based on the fact that when the data for the wild gray Norway (*reference table 187*) are compared with the data for the Albino (*reference table 144*), using the body lengths found for the captive Grays at G_{10} , the wild gray Norway surpasses the Albino in brain weight by 15 per cent in the males and 14 per cent in the females. It is evident, therefore, that the reduction of the brain weight of the captive Grays at G_{10} , which is 5 per cent or less in both sexes, marks only a slight shift toward the relations characteristic for the Albino. To determine whether the low brain weights characteristic of the Albinos were shown by any individuals among the captive Grays, the graphs in charts 15 and 16 have been prepared. The limiting graphs give the extreme deviations plus and minus for each

sex in each generation. In a general way, these graphs for the extremes follow those for their respective means. They show also that in the case of the males a deficiency of 15 per cent or more occurs five times, while in the case of the females a deficiency of 14 per cent or more occurs three times. Thus, some individuals do deviate as much as do the Albinos on the average, but, as the results show, these extreme deficiencies have not sufficient frequency to produce more than a slight average deficiency in the case of the captive Grays.

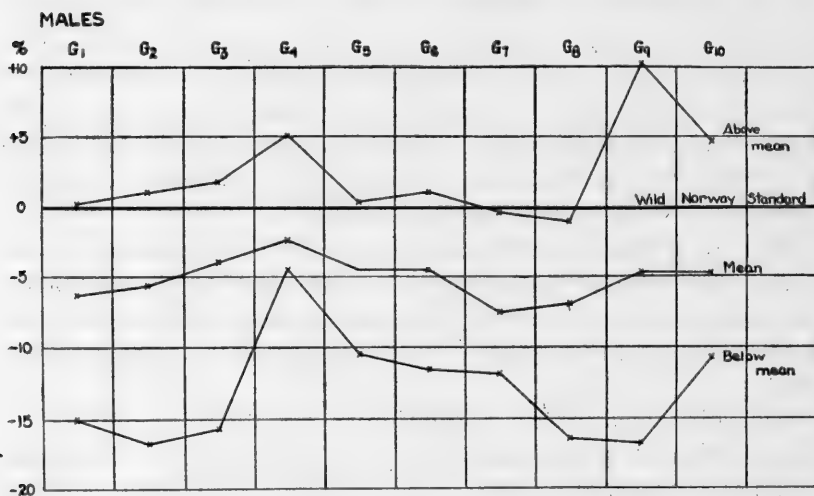


Chart 15 Brain weight: Deviations of limiting values above and below the mean in each generation of captive Grays. Males.

Parts of the brain

The percentages of the brain weight represented by the olfactory bulbs and by the paraflocculi are given in table 15 and chart 14. The relations of these percentages can be briefly stated. In both instances the average of the percentage values for the female runs a trifle below that for the male, but in both sexes and for both parts these values remain nearly constant from G₁ to G₁₀. It follows from this that the fluctuations in the weight of the entire brain are accompanied by corresponding fluctuations in the weights of these parts, thus maintaining constant weight relations.

From this study we conclude, therefore, that captivity for ten generations has reduced the brain weight of the test Grays only by 5 per cent in the males and 3 per cent in the females. The shift is toward the relations characteristic for the Albino, but still leaves some 10 or 11 per cent to go. The data as they stand do not show any marked tendency to a progressive reduction in brain weight. As to the parts of the brain here examined, these vary as does the remainder of the brain, and hence retain a constant percentage weight.

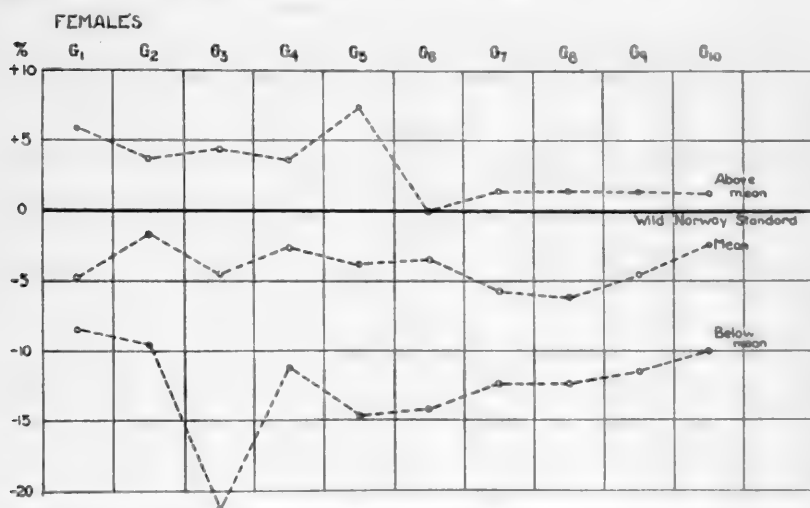


Chart 16 Brain weight: Deviations of limiting values above and below the mean in each generation of captive Grays. Females.

ON THE WEIGHT OF THE HYPOPHYSIS IN THE CAPTIVE GRAYS

Standards: Data in *reference table 148* for the Albino and data in *table 205* for the wild Norway. The hypophysis is lighter in the wild gray Norway than in the Albino. This difference is specially marked in the female hypophysis.

The deviations in the weight of the hypophysis of the captive Grays from albino standards are given in tables 16, 17, and 18 and chart 17. The course of the graphs for the two sexes is similar. When the base line used for reference repre-

sents male albino values, then the values for the male captive Grays, graph 1, run from 10 to 20 per cent minus, while the values for the female captive Grays (3) run about 5 to 10 per cent plus. When, however, the base line in chart is taken as representing the standard values for the female Albino, then the values for the female captive Grays run from 50 to 60 per cent low (graph 2, chart 17).

If the sag which occurs in the graphs at G_6 and G_7 is neglected, the graphs give no evidence for a progressive change in the weight of the hypophysis in the later generations. Nevertheless, at G_9 there is, in both sexes, a conspicuously high value that is noteworthy and may be significant.

TABLE 15

Weights of bulbs and of paraflocculi together with their respective percentage weights on the entire brain. (Chart 14, A and B)

GENERATION	NUMBER OF CASES	BULBS (A)		PARAFLOCCULI (B)	
		Observed	Per cent brain weight	Observed	Per cent brain weight
Males					
		<i>Grams</i>		<i>Grams</i>	
G ₃	10	.0868	3.88	.0342	1.54
G ₄	27	.1064	4.57	.0329	1.40
G ₅	20	.0958	4.35	.0322	1.46
G ₆	20	.0976	4.34	.0324	1.44
G ₇	23	.1045	4.78	.0323	1.48
G ₈	21	.0902	4.20	.0320	1.49
G ₉	20	.0985	4.50	.0329	1.50
G ₁₀	20	.0947	4.24	.0333	1.51
		Average:	4.36	Average:	1.48
Females					
G ₃	17	.0745	3.54	.0304	1.46
G ₄	24	.0945	4.39	.0298	1.38
G ₅	18	.0864	4.21	.0306	1.46
G ₆	18	.0947	4.36	.0299	1.38
G ₇	21	.0911	4.37	.0305	1.44
G ₈	22	.0922	4.49	.0276	1.29
G ₉	19	.1002	4.77	.0303	1.44
G ₁₀	21	.0914	4.27	.0320	1.50
		Average:	4.29	Average:	1.42

TABLE 16

On the weight of the hypophysis in the captive Grays and the deviations from the corresponding standards for body weight and body length.

(Chart 17 (1).) *Males*

GENERATION	NUMBER OF CASES	HYPOPHYSIS				
		Observed	On body weight	On body length	Percentage deviations	
					On body weight	On body length
		<i>Grams</i>	<i>Grams</i>	<i>Grams</i>	<i>%</i>	
G ₁	23	.0112	.0118	.0125	— 5.3	— 10.0
G ₂	40	.0096	.0112	.0119	— 14.1	— 18.7
G ₃	18	.0105	.0122	.0123	— 13.9	— 14.6
G ₄	27	.0112	.0126	.0135	— 11.1	— 17.0
G ₅	20	.0099	.0115	.0118	— 13.9	— 16.1
G ₆	20	.0104	.0124	.0135	— 16.1	— 23.0
G ₇	23	.0103	.0126	.0133	— 18.3	— 22.6
G ₈	21	.0099	.0119	.0121	— 16.8	— 18.2
G ₉	20	.0107	.0125	.0118	— 14.4	— 9.3
G ₁₀	20	.0091	.0122	.0123	— 25.4	— 26.0

TABLE 17

On the weight of the hypophysis in the captive Grays and the deviations from the corresponding standards for body weight and body length.

(Chart 17 (2).) *Females*

GENERATION	NUMBER OF CASES	HYPOPHYSIS				
		Observed	On body weight	On body length	Percentage deviations	
					On body weight	On body length
		<i>Grams</i>	<i>Grams</i>	<i>Grams</i>		
G ₁	18	.0109	.0195	.0238	— 44.3	— 54.3
G ₂	26	.0104	.0184	.0210	— 43.4	— 50.4
G ₃	26	.0104	.0191	.0221	— 45.6	— 52.9
G ₄	24	.0104	.0190	.0229	— 45.3	— 54.6
G ₅	18	.0104	.0196	.0216	— 46.9	— 51.9
G ₆	18	.0110	.0236	.0265	— 53.4	— 59.0
G ₇	21	.0102	.0205	.0232	— 50.2	— 56.0
G ₈	22	.0107	.0219	.0238	— 51.1	— 55.0
G ₉	20	.0117	.0213	.0223	— 45.1	— 47.5
G ₁₀	21	.0099	.0217	.0221	— 54.4	— 55.2

TABLE 18

Hypophysis weights. Deviations of female values for the captive Grays when referred to male albino standards. (Chart 17 (3).) Females

GENERATION	NUMBER OF CASES	HYPOPHYSIS		
		Observed	On body length	Percentage deviations
		Grams	Grams	
G ₁	18	.0109	.0102	+ 6.4
G ₂	26	.0104	.0090	+ 13.4
G ₃	26	.0104	.0097	+ 6.7
G ₄	24	.0104	.0102	+ 1.9
G ₅	18	.0104	.0095	+ 8.6
G ₆	18	.0110	.0112	- 1.7
G ₇	21	.0102	.0102	0
G ₈	22	.0107	.0102	+ 4.9
G ₉	20	.0117	.0101	+ 13.6
G ₁₀	21	.0099	.0097	+ 2.0

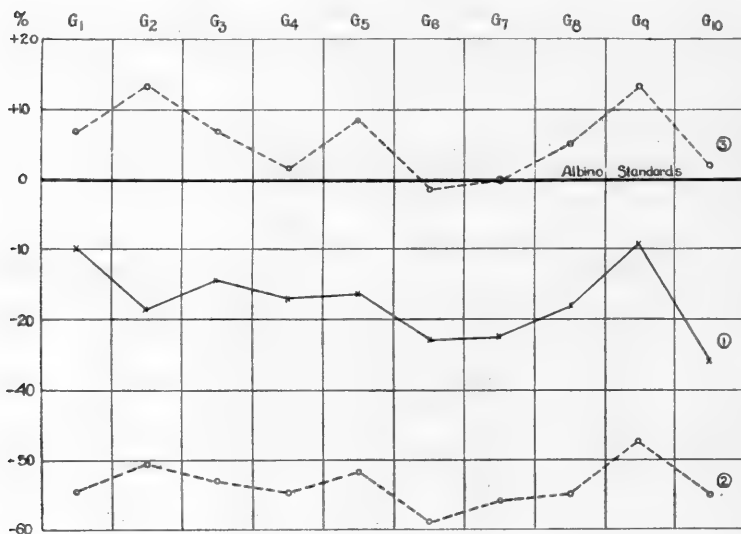


Chart 17 Hypophysis weight: Deviations in captive Grays on body length—Albino standards.

1. For male—when standard Albino values are for the male.
2. For female—when standard Albino values are for the female.
3. For female—when standards are as in 1.

When the percentage weight of the hypophysis on the weight of the brain (data for brain weight in tables 13 and 14 and for the hypophysis weight in tables 16 and 17) is computed, the values obtained are represented by the graphs in chart 18. These graphs show the percentage value of the hypophysis to be higher in the female than in the male, but on the whole the graphs for both sexes are nearly horizontal, indicating a constancy in the percentage values.

To determine whether the weight relations of the hypophysis in the captive Grays have been changed from those shown by the wild strain, the weights for the former have been compared with those for the latter as given in *table 205*. When

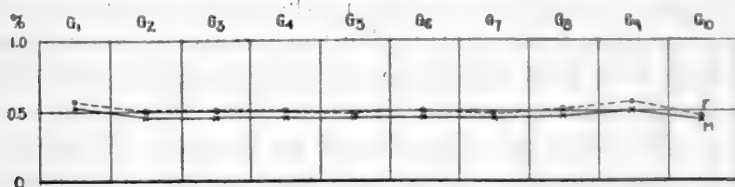


Chart 18 Percentage weight of hypophysis on observed brain weight in captive Grays—both sexes. —, male; ---, female.

the data in that table are revised in terms of body length, it appears that the weight of the hypophysis in the captive Grays runs above that for the wild strain by about 7 per cent in the males and 11 per cent in the females. Thus, the weight of the hypophysis has apparently increased slightly in both sexes of the captive Grays. This is a shift toward the albino values. At the same time the weight relations according to sex remain in the captive Grays similar to those found in the wild strain, and the female hypophysis shows no tendency to the very heavy weight characteristic of the albino females.

ON THE WEIGHT OF THE THYROID IN THE CAPTIVE GRAYS

Standards: *Reference table 148* for the Albino and *table 204* for the wild gray Norway. The thyroid has about the same weight in the wild gray Norway and the Albino.

The percentage deviations in the weight of the thyroid are given in tables 19 and 20. The graphs appear in chart 19.

A word of explanation touching the standard albino record is necessary. The values are from *reference table 148*. This table was made some fifteen years ago, when the Albinos used for it were living under less favorable conditions than those at present obtaining in our colony. One result of the improved treatment has been to diminish the weight of the thyroid in the Albino, so that to-day, at the body length of the captive Grays, the observed values for albino thyroid are 52 per cent below the reference-table values for the males and 53 per cent below for the females.

Inspection of chart 19 shows a progressive diminution in the weight of the thyroid with some fluctuations. In general, the graphs for the two sexes run the same course, but the average percentage deviation for the females is about 1 per cent more than that for the males. This relation, according to sex, calls for a word of comment. On body length the weights for the female thyroids of the standard Albino surpass those for the males by about 7 per cent, while in the wild strain this sex difference does not appear.

Since the basal values for the female Albino are 7 per cent higher than for the male and since the thyroid weight in the captive Grays is only 1 per cent below that of the males when thus charted, it follows that in the captive Grays the thyroid on body length is heavier in the females than in the males. There is thus a shift toward the sex relations found in the Albino.

When compared with the data in *table 204* (reduced to the body-length basis), it appears that the wild gray Norways have thyroid weights close to those for the Albino. From this it follows that the deviation in weight shown by G_1 of the captive Grays probably represents a marked loss in thyroid weight from that for the wild ancestors. It is evident that in the case of the thyroid there is a progressive loss in weight, in both sexes, from G_1 to G_{10} . This has occurred during the period of captivity and might be regarded as an effect of captivity were it not for the behavior of the thyroid in the Albino. In 1912, this albino strain, after many years in

captivity, gave thyroid weights as entered in *reference table 148*. Since then, however, the weight of the thyroid in these domesticated Albinos has shown a marked diminution and to-day (at the body lengths of the captive Grays) is only some 48 per cent (male) and 47 per cent (female) of its original table value. Here, then, is a marked change in the thyroid weight of the Albino occurring after many generations in captivity. This must be due to some special condition, and it seems most probable that some change in the food or its method of preparation has acted as the cause.

It appears, therefore, that the weight of the thyroid undergoes a progressive decrease in the captive Grays, probably in response to some special food conditions. There is a sag in the graphs at G_3 and G_7 . The final weight values at G_{10} drop below those for the Albino as given by our current records, while the weight relations according to sex become those for the albino strain (i.e., on body length the female thyroid is heavier).

In this connection we enter some observations by Miss Meeser on structural deficiencies observed in the thyroid and

TABLE 19
Thyroid weights in the captive Grays and deviations from the corresponding standards on body weight and body length. (Chart 19.)
Albino standard. Males

GENERATION	NUMBER OF CASES	THYROID				
		Observed	On body weight	On body length	Percentage deviations	
					On body weight	On body length
		<i>Grams</i>				
G_1	15	.0301	.0501	.0540	— 39.9	— 44.2
G_2	34	.0320	.0477	.0493	— 32.9	— 35.1
G_3	17	.0315	.0533	.0533	— 40.5	— 40.9
G_4	27	.0301	.0560	.0601	— 46.2	— 39.9
G_5	20	.0257	.0495	.0499	— 48.0	— 48.4
G_6	20	.0264	.0544	.0585	— 51.4	— 54.8
G_7	23	.0248	.0548	.0577	— 54.7	— 57.0
G_8	21	.0248	.0516	.0512	— 51.9	— 51.5
G_9	20	.0265	.0536	.0506	— 50.5	— 47.6
G_{10}	20	.0235	.0538	.0519	— 56.3	— 54.7
					Average:	— 47.41

TABLE 20

Thyroid weights in the captive Grays and deviations from the corresponding standards on body weight and body length. (Chart 19.)
Albino standard. Females

GENERATION	NUMBER OF CASES	THYROID				
		Observed	On body weight	On body length	Percentage deviations	
					On body weight	On body length
		<i>Grams</i>				
G ₁	7	.0344	.0413	.0467	— 16.7	— 26.3
G ₂	22	.0272	.0391	.0414	— 30.4	— 34.3
G ₃	26	.0232	.0405	.0443	— 42.7	— 47.6
G ₄	24	.0197	.0401	.0467	— 50.8	— 57.8
G ₅	18	.0213	.0414	.0437	— 48.5	— 51.2
G ₆	18	.0227	.0472	.0480	— 51.9	— 52.7
G ₇	21	.0201	.0427	.0467	— 54.9	— 56.9
G ₈	22	.0224	.0447	.0467	— 49.9	— 52.0
G ₉	20	.0252	.0451	.0461	— 44.1	— 45.3
G ₁₀	21	.0171	.0445	.0443	— 61.5	— 61.4
					Average:	— 48.53

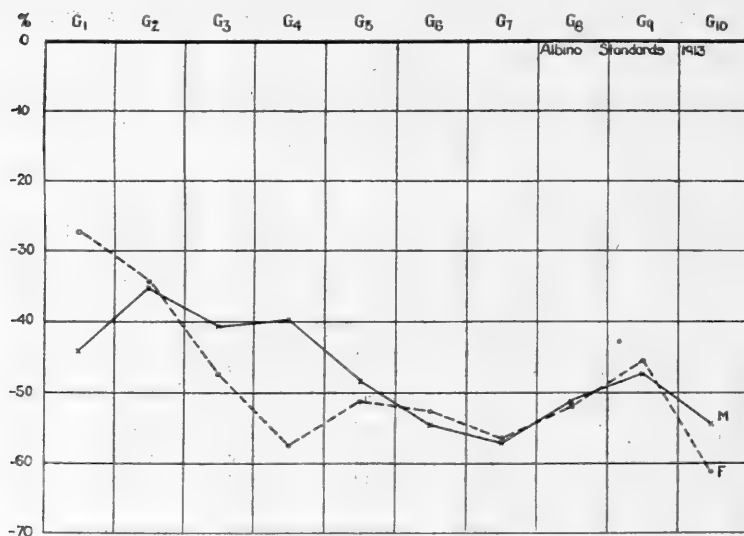


Chart 19 Thyroid weight in captive Grays. Percentage deviation in weight of thyroid on body length—Albino standards—1913. (Tables 19 and 20.)

parathyroid glands. Her dissection records show the relations given in table 21.

It appears that in the generations of captive Grays from G_2 to G_{10} the thyroid was missing on one side in twelve cases and defective in two others. The total number of rats examined was 449. In five cases the corresponding parathyroid was also missing. In thirteen out of fourteen cases the defect was on the right side, and twelve of the fourteen rats were females. Here is a series of defects, in the thyroid and parathyroid, which occur predominately in females and on the right side. The parathyroid is missing in less than half the cases. Four of these five cases of missing parathyroid were in G_{10} .

The skulls which were prepared from this generation showed several instances of defective incisors—a condition probably related to deficiency in parathyroid secretion (Hammett, '22). It may be said, further, that these structural defects seem, so far, to be a peculiarity of this series of captive Grays and have been noted heretofore only in one instance, a hybrid—Norway \times Albino—out of hundreds of rats dissected.

TABLE 21

Record of deficiencies in the thyroid and parathyroid glands. Captive Grays—fourteen cases

GENERATION	SEX	THYROID		PARATHYROID	
		Side	Condition	Side	Condition
G_2	F	L	Almost gone	L	Present
G_4	F	R	Missing	R	Present
G_4	F	R	Missing	R	Present
G_5	M	R	Missing	R	Enlarged
G_5	F	R	Missing	R	Present
G_5	F	R	Very tiny	R	Present
G_6	M	R	Missing	R	Missing
G_7	F	R	Missing	R	Present
G_8	F	R	Missing	R	Present
G_9	F	R	Missing	R	Present
G_{10}	F	R	Missing	R	Missing
G_{10}	F	R	Missing	R	Missing
G_{10}	F	R	Missing	R	Missing
G_{10}	F	R	Missing	R	Missing

WEIGHT OF BOTH SUPRARENALS IN THE CAPTIVE GRAYS

Standards: *Reference table 148* for Albino and *table 206* for wild gray Norways. In both the Albino and the wild gray Norway the weight of the suprarenals is much greater in the female than in the male.

In the wild strain the weights in both sexes are greater than in the Albino.

The percentage deviations in the weight of the suprarenals (both glands) are given for the captive gray males in table 22 and for the females in table 23. The graphs for the deviations on body length are entered in chart 20. Inspection of



Chart 20 Weight of suprarenals in captive Grays. Percentage deviations in weight of suprarenals on body length, both sexes—Albino standards.

the graphs shows similar trends in the deviations for the two sexes. The sag from G₆ to G₈ is very marked, but neglecting this there is no tendency for a progressive diminution in the weight of the suprarenals as between the earlier and later generations.

It should be noted that, in the case of the Albino, the weight of the suprarenals in the female exceeds that in the male by about 90 per cent for the body lengths here considered. In the case of the captive Grays, however, the female suprarenals are in excess by only about 41 per cent. When, therefore, the deviations based on the albino standards for each sex are plotted on the same chart, as is here done, the graph for the female necessarily runs below that for the male.

To determine the difference in relations between the captive Grays and wild gray Norways, the data for the former have been compared with those given in *table 206*. Such a comparison shows that in the captive Grays the weights of the suprarenals are, on the average, less than in the wild strain by some 21 per cent in the males and 32 per cent in the females. The suprarenals in the captive Grays have thus lost weight as compared with those in the wild strain, and the greater loss is shown by the females.

We conclude, therefore, that captivity has reduced the weight of the suprarenals in the captive Grays, and that this reduction is more marked in the female. Such reductions represent a shift toward the weight values for the Albino. The weight relations according to sex are, however, brought closer in the captive Grays, and hence, away from the relation found both in the Albino and in the wild Gray. Thus the female suprarenals appear to be more responsive than those of the male. Finally, after the distinct drop between the values for the wild form and G_1 , the graphs in chart 20 do not show a progressive diminution in weight from G_1 to G_{10} , but they do show a high degree of response to unfavorable conditions from G_6 to G_8 —a feature of some importance.

TABLE 22

Suprarenal weights (both glands) in the captive Grays and deviations from the corresponding standards on body weight and body length. (Chart 20.)

Albino standards. Males

GENERATION	NUMBER OF CASES	OBSERVED WEIGHT	ON BODY WEIGHT	ON BODY LENGTH	PERCENTAGE DEVIATION	
					On body weight	On body length
G ₁	23	.0707	.0501	.0525	+ 41.1	+ 34.7
G ₂	40	.0736	.0488	.0517	+ 50.8	+ 42.4
G ₃	17	.0766	.0523	.0521	+ 46.5	+ 47.0
G ₄	27	.0786	.0530	.0561	+ 48.3	+ 40.1
G ₅	20	.0700	.0491	.0501	+ 42.6	+ 39.7
G ₆	20	.0662	.0524	.0560	+ 26.3	+ 18.2
G ₇	23	.0701	.0528	.0552	+ 32.8	+ 27.0
G ₈	21	.0650	.0505	.0510	+ 28.7	+ 27.5
G ₉	20	.0754	.0527	.0501	+ 43.1	+ 50.5
G ₁₀	20	.0727	.0517	.0519	+ 40.6	+ 40.1
					Average:	+ 36.72

TABLE 23

Suprarenal weights (both glands) in the captive Grays and deviations from the corresponding standards on body weight and body length. (Chart 20.)

Albino standards. Females

GENERATION	NUMBER OF CASES	OBSERVED WEIGHT	ON BODY WEIGHT	ON BODY LENGTH	PERCENTAGE DEVIATION	
					On body weight	On body length
G ₁	18	.0888	.0695	.0832	+ 27.8	+ 6.8
G ₂	26	.0881	.0652	.0727	+ 34.8	+ 21.6
G ₃	26	.1002	.0692	.0783	+ 44.8	+ 28.1
G ₄	24	.0997	.0692	.0810	+ 44.1	+ 23.1
G ₅	18	.0947	.0708	.0761	+ 33.8	+ 23.5
G ₆	18	.0917	.0828	.0925	+ 10.8	— 0.9
G ₇	21	.0789	.0735	.0821	+ 7.4	— 3.9
G ₈	22	.0857	.0778	.0832	+ 10.2	+ 3.0
G ₉	20	.0892	.0763	.0791	+ 16.8	+ 12.8
G ₁₀	21	.0920	.0771	.0783	+ 19.3	+ 17.5
					Average:	+ 13.64

WEIGHT OF GONADS IN THE CAPTIVE GRAYS

Standards: *Reference table 146* for the Albino and *table 207* for the wild gray Norway. In both sexes the gonads in the wild gray Norway are heavier than in the Albino.

The percentage deviations in the weights of the gonads, on albino standards, are given in table 24. The corresponding graphs, on body length, are entered in chart 21.

TABLE 24

Weight of gonads in the captive Grays and deviations from corresponding standards on body weight and body length. (Chart 21.) Albino standards

GENERATION	NUMBER OF CASES	STANDARDS				
		Observed	On body weight	On body length	Percentage deviations	
					On body weight	On body length
Testes						
G ₄	27	3.548	2.985	3.093	18.9	14.7
G ₅	20	3.013	2.841	2.825	6.1	6.7
G ₆	20	3.441	2.969	3.092	15.9	11.3
G ₇	23	3.354	2.981	3.063	12.5	9.5
G ₈	21	3.715	2.899	2.916	28.2	27.4
G ₉	20	3.458	2.980	2.884	16.0	19.9
G ₁₀	20	3.894	2.963	2.945	31.4	32.2
					Average: + 17.4	
Ovaries						
G ₄	24	.0985	.0505	.0515	95.1	91.3
G ₅	18	.1017	.0506	.0510	101.0	99.4
G ₆	18	.1173	.0515	.0520	127.8	125.6
G ₇	21	.0968	.0509	.0515	90.2	88.0
G ₈	22	.1119	.0512	.0515	118.6	117.3
G ₉	19	.0953	.0513	.0515	85.8	85.1
G ₁₀	21	.1024	.0512	.0512	100.0	100.0
					Average: + 100.9	

The records do not begin until G₄. As shown in chart 21, the graphs for the two sexes exhibit the same trends, save at G₅. This suggests that the influences affecting the weight of the gonads act in a similar manner in both sexes.

As compared with the albino standard, the data for the captive Grays average 17 per cent higher for the testes and 101 per cent higher for the ovaries.

A comparison of the data for the wild strain, *table 207*, with those for the captive Grays indicates that these latter run about 1 per cent higher in the male and 8 per cent higher in the female. No significance is to be attached to these dif-

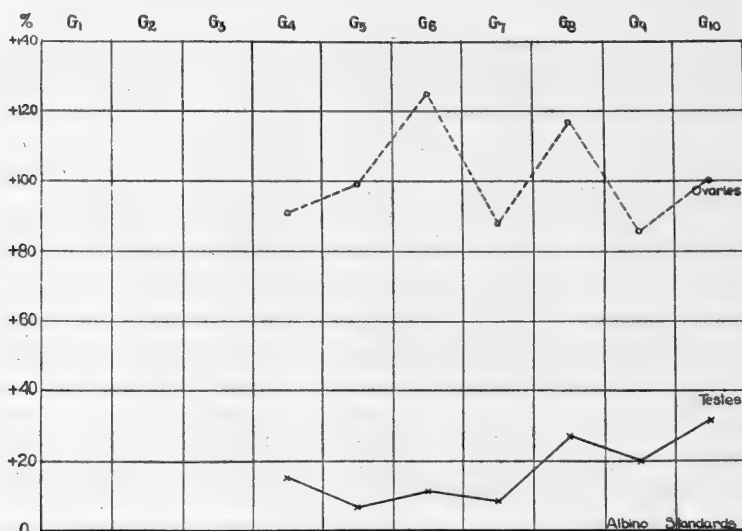


Chart 21 Percentage deviations in the weight of the gonads in captive Grays: Ovaries: testes. Albino standards.

ferences in themselves, but they serve to indicate that no important modification has been made in the weights of the gonads. Thus, from G_4 to G_{10} the gonads remain as in the wild strain and, therefore, show no tendency to assume the albino values which run much lower in both sexes. Nevertheless, while there is no evidence for the influence of the unfavorable conditions on the weight of the testes, there is perhaps some evidence at G_5 , G_6 , and G_7 for a depression in the weight of the ovaries.

PART II, SERIES 2. ON THE PARTS OF THE SKELETON IN THE CAPTIVE GRAYS

Before discussing the effects of captivity, as just presented in series 1, the observations on the parts of the skeleton, series 2, will be considered.

The rats used for this series were from the same generation groups as those examined in series 1. They were, however, different individuals, and the data do not become available until G_4 .

With two exceptions, the averages used were based on five individuals in each sex group in each generation. The dissections were all by Miss Ruth Meeser. Using this material, the following determinations have been made: 1) the weight; 2) the length, and, 3) the percentage of water for the cranium, mandible, humerus, and femur.

The purpose of these observations was to determine whether there were any progressive changes taking place in the bones of the captive Grays between G_4 and G_{10} and also to determine whether such changes indicated a shift toward the values for the Albino. In the absence of corresponding observations on the wild strain, the relations of the captive Grays to this strain could not be determined.

The relations found have proved to be so similar in all the four parts of the skeleton examined that the data for the femur, which are typical, will alone be presented here.

The standard values used for the several base lines are from *reference tables 131, 128, and 163* for the Albino. The computed deviations are given in table 25 and plotted in chart 22.

Examination of the graphs shows that the deviations in the length of the femur are slight and those that occur are mainly retardations in response to unfavorable conditions. The deviations in weight are, however, large, and the retarda-

tions at G_5 , G_6 , and G_7 are clearly marked. At the same time, the deviations in the percentage of water follow the deviations in weight. On considering these changes together, it appears that when the femur is less in weight the medullary cavity also becomes less, and as this cavity carries water-bearing materials the percentage of water is thereby diminished. The deviation in the percentage of water in this case

TABLE 25

Giving the percentage deviations for the weight, length, and percentage of water in the femur of the captive Grays

GENERATION	SEX	AGE	BODY LENGTH	PERCENTAGE DEVIATIONS		
				Weight (fresh)	Length (fresh)	Per cent water
			<i>Mm.</i>			
G_4	M	523	233	+ 29.3	+ 0.3	+ 14.1
	F	516	222	+ 33.6	— 1.0	+ 13.0
G_5	M	590	234	+ 20.0	— 5.0	+ 0.9
	F	602	230	+ 12.1	— 2.0	— 0.3
G_6	M	559	251	+ 26.1	— 1.3	— 0.3
	F	599	231	+ 14.8	— 3.0	— 3.1
G_7	M	583	235	+ 22.5	— 3.0	— 0.05
	F	606	218	+ 14.8	— 8.0	+ 5.4
G_8	M	578	242	+ 34.5	+ 2.0	+ 7.5
	F	592	226	+ 23.3	+ 2.0	+ 8.9
G_9	M	606	230	+ 38.7	— 1.4	+ 6.9
	F	601	222	+ 31.2	— 2.0	— 4.0
G_{10}	M	598	229	+ 33.4	— 0.2	— 4.9
	F	591	223	+ 31.7	— 2.1	+ 2.5

is, therefore, not to be referred to the osseous tissue in the strict sense, but to the entire bone as an organ.

There is one feature in these graphs that calls for comment, namely, the frequency of low values at G_5 . In series 1 the first low value marking a sag in the graph usually comes at G_6 . We infer from this relation that the unfavorable conditions which are assumed to produce these retardations are effective in modifying the skeleton in animals that are older than those in which the several organs are affected (chart 1).

It appears, therefore, that between G_4 and G_{10} the various parts of the skeleton show no progressive changes in the characters measured. Whether there has been a lowering of values previous to G_4 our data do not indicate. These parts of the skeleton do show retardations under unfavorable conditions, and the response can apparently be obtained in rats that are younger than those that show organ changes.

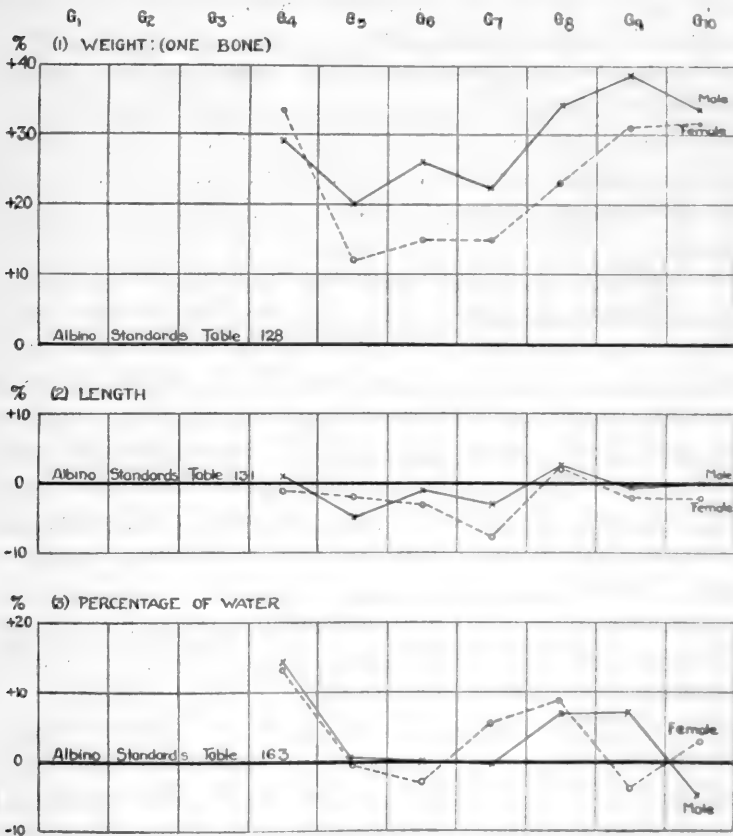


Chart 22 Data on femur: Percentage deviations on body length in captive Grays of, 1) weight; 2) length; 3) percentage of water—Albino standards.

DISCUSSION

Attention is called to the fact that the data here to be considered are from the first ten generations only of gray Norway rats in captivity. To obtain the full effects of captivity on the body and its organs will probably require many more generations, and, therefore, any conclusions drawn from the present data must be largely tentative.

Body size. This is best measured by body length, and chart 12 gives the graph for the observed values. As the entries in tables 11 and 12 show, the body length at G_1 is for rats much over 600 days of age and at G_2 for those under this age, while the remaining eight entries run close to 600 days. Correction for age would bring down the body length at G_1 and slightly raise it at G_2 . Both changes are small, however.

If the graphs for body length are viewed with these possible corrections in mind, it is seen that the values for the first three generations are low, but, in both sexes, giving average values not essentially different from those for the last three generations. Moreover, the unfavorable conditions which were acting from G_5 to G_8 do not produce any clear-cut effects as indicated by these graphs. The mean body-length value for the series is 240 mm. for the males and, for the females, 223 mm. Captivity has, therefore, not altered the *body length on age*.

Body weight. In chart 13 the relations of the body weights as observed to those to be expected on the observed body length (*reference table 187*) are shown by the graphs. The graphs also show that the observed values exceed the tabular values for the wild gray Norways and that the excess tends to increase in the successive generations, so that at G_{10} the body weights of the captive Grays are in excess by 16.6 per cent in the males and by 16.2 per cent in the females. This excess in body weight is similar to that shown by the Albinos, so that captivity for ten generations has developed in the captive Grays the weight-length relations which are characteristic for the Albino. However, the graphs sag slightly

at G_6 and G_7 in response to the unfavorable conditions then acting.

To summarize the foregoing: In captivity for ten generations the gray rat shows a constant body length on age, but a weight-length relation which differs from that for the wild Norway, and agrees at G_{10} with that for the Albino. These captive Grays, then, are rats which grow normally in length, but tend to become fatter as the generations progress.

In these captive Grays the weights of the brain, hypophysis, thyroid, and suprarenals have been followed from G_1 to G_{10} .

Brain weight. As to these values in the ancestors of this series little can be said. The brain weight for the male ancestors was that expected for the wild gray Norway, *reference table 187*, but for the female ancestors it was 2.5 per cent low. The G_1 values are definitely lower, as shown in chart 14. This drop at G_1 is followed by a recovery in weight, which runs into a sag at G_7 and G_8 and then again recovers. On the average, both sexes show brains 5 per cent or less below the standard for the wild gray Norway, but within the ten generations there has been no progressive diminution in weight. It appears, therefore, that the conditions of captivity cause an immediate drop (G_1) in brain weight, but within ten generations this drop does not further increase.

Hypophysis weight. When compared with the data for the wild strain, the observations on the captive Grays show a tendency to an increase in weight, the values for the males running 7 per cent and for the females 11 per cent above those for the wild strain. Thus, although there is a sag in the graphs at G_6 and G_7 and no progressive change in weight, there appears to be in the hypophysis a slight increase in weight as the result of captivity. So far as this goes it is a shift toward the relations in the Albino, but it does not go far enough to produce the very heavy female hypophysis characteristic of the Albino.

Thyroid weight. The thyroid gland is the only organ thus far found in which there is a progressive loss in weight. In

G_1 the weight is already reduced below the reference-table value, and the reduction, with a slight intensification at G_6 and G_7 , continues to G_{10} . This weight change is certainly an effect of captivity in the broad sense, but is most probably due to a special condition represented by the food, and not to the more general conditions surrounding the captive animal. In this sense the response of the thyroid seems a bit peculiar and different from those made by the other organs. At G_{10} the thyroid in the captive Grays has weights close to those now current in this laboratory for the Albino. Structural defects in the thyroid and in the parathyroid were also noted (table 21).

Suprarenal weights. Already at G_1 the weight of the suprarenals is low. Then follows a recovery in weight which is interrupted by a retardation of growth at G_6 , G_7 , and G_8 , to be once more followed by a recovery that reaches about the initial values. Thus, there is no progressive change in weight. As compared with the wild strain, the captive Grays have distinctly smaller suprarenals in both sexes, thus approaching the relations in the Albino, but the weight relations according to sex are shifted away from those in the Albino, since the weights according to sex come nearer together. The suprarenals are conspicuous, however, in the fullness of their response to unfavorable conditions. They apparently act as a sort of physiological barometer, registering directly the pressure of unfavorable conditions by a retardation in their growth.

This completes the examination of the weight changes in the four organs studied from G_1 to G_{10} . There remain the gonads and the parts of the skeleton (series 2) for which data are available only from G_4 to G_{10} . Obviously, in these cases nothing can be said about the initial drop in weight at G_1 , and it is possible to compare only the G_4 with the final values and to record any indication of the effect of unfavorable conditions.

Gonads: weight. The graphs in chart 21 show that in the testes the G_4 and final weights are similar. There is no

indication of the influence of unfavorable conditions, and the weights for the captive Grays are similar to those for the wild strain. Thus, there is no modification in the weights bringing these down to those of the Albino. On the whole, captivity and unfavorable conditions appear to have produced less effect on the testes than on any other organ studied.

In the case of the ovaries, the weights remain as high or even a little higher than in the wild strain, but in contrast to the testes the ovaries do seem to respond to the unfavorable conditions with lower values at G_5 and G_7 . The failure of the gonads to change in weight during the first ten generations of captivity was unexpected, in view of the much lower weight values for the gonads shown by the Albinos.

Parts of the skeleton (series 2), table 25, chart 22

Length, weight, and percentage of water. Femur. As noted in the previous consideration of the data in series 2, the various parts and bones examined for length, weight, and percentage of water agree in their general behavior with one another. For this reason it was deemed sufficient to note in detail the results for the femur. Between G_4 and G_{10} there is, in the femur, no progressive change in length, weight, or percentage of water. The unfavorable conditions are marked by low values in each of these characters from G_5 to G_7 . We have no reference tables for these characters in the wild strain, but, as the results stand, the femur in the captive Gray is distinctly heavier and has about the same length and a slightly greater percentage of water than in the Albino. Under unfavorable conditions, the femur becomes more slender (i.e., the weight is more reduced than the length), the cavity is diminished, and the percentage of water decreased. All that can be said in a general way is that there is no progressive change in these characters between G_4 and G_{10} . The striking result in this case is the great susceptibility of the osseous system—as represented by the femur—to unfavorable conditions, to which it responds with marked reductions in weight and in percentage of water.

Using the data for the wild gray rat as standards, the effects of captivity for ten generations on the gray Norway rat, as shown by the foregoing data, may be formulated as follows:

1. Body length on age is not modified.
2. Body weight on body length increases progressively and at G_{10} has the relation found in the Albino.

3. In the organs:

- a. An initial drop in weight (ancestors to G_1) apparently occurs in the brain, thyroid, and suprarenals. It cannot be determined in the gonads or bones, as the G_1 values are not available.

- b. Progressive loss in weight is shown by the thyroid—the only organ behaving this way. This is probably due to the character of the food.

- c. A slight increase in weight is shown by the hypophysis.

- d. No progressive loss in weight between G_1 (or G_4) and G_{10} occurs in the brain, hypophysis, suprarenals, gonads, or bones.

- e. A shift in the weight values toward those characteristic for the Albino is shown by the brain, hypophysis, thyroid, and suprarenals. This point cannot be determined in the case of the bones.

4. Unfavorable conditions, represented by louse infection, delousing, high temperature, and poor care (chart 1), are associated with low values in the graphs, except in the cases of body length and of the testes. Table 26 gives the generations in which low values appear in the several instances. In the seven cases in which a response occurs it always appears at G_7 and, with the exception of the brain, always at G_6 , but in two instances, the ovaries and the bones, it is seen also at G_5 and in another two instances, brain and suprarenals, at G_8 . The interpretation of the two extreme groups is that, in the case of the ovaries and the bones, unfavorable conditions can modify the weight even after growth is well advanced, while in the case of the brain and suprarenals the modification is either through the young themselves or even through effects on the parents.

5. Sex differences in weight.

In the Albino, sex differences in weight are conspicuous in the hypophysis and suprarenals, the gland in the female being much heavier in each case.

In the captive Gray:

Hypophysis: The sex weight relation changes slightly, giving a somewhat heavier hypophysis in the female captive Gray. This is the Albino relation.

TABLE 26

To show the generations in which low values occur in the several instances

	GENERATION			
	G ₅	G ₆	G ₇	G ₈
Body weight		X	X	
Body length				
Brain			X	X
Hypophysis		X	X	
Thyroid		X	X	
Suprarenals		X	X	X
Testes				
Ovaries	X	X	X	
Femur	X	X	X	

X indicates a low value.

Suprarenals: The weight of the female gland is brought closer to that for the male. This is a shift away from the relations for both the wild Norway and the Albino.

6. All these determinations have been made on animals approximately 600 days old (equivalent to 50 years in human age). The values studied are terminal values, and it is possible to determine only indirectly, as by the effect of unfavorable conditions, at what phase of growth the various modifications occurred.

7. The larger results are these: In only one organ, the thyroid, is there a progressive loss in weight, and this is most probably due to food. One organ, the hypophysis, increases

in weight slightly. Unfavorable conditions produce organs of smaller weight, but though this response takes place, the body length remains unchanged and the body weight is but slightly affected.

CONCLUSIONS

After ten generations in captivity, the captive Gray differs from the wild type as follows:

There is an increase in body weight on body length. A slight increase in the weight of the hypophysis. No change occurs in the weights of the gonads. Less in weight are the brain, the thyroid, and the suprarenals, especially the female suprarenals.

In organs of lesser weight the greater loss occurs at G_1 , but there is no subsequent progressive loss, save in the thyroid.

Similarly, the captive Gray compared with the Albino shows the following relations:

The brain, the suprarenals (especially in the male), the gonads, and the bones are still heavy. Body weight on body length and the weight of the thyroid are similar to those for the Albino.

The hypophysis, especially that of the female, remains less in weight.

Ten generations of captivity have, by no means, served to give the captive Grays the organ constitution of the Albino.

In view of the preliminary character of this report, no survey of the literature will be attempted at this time.

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